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TRANSACTIONS AND PROCEEDINGS

OF THE

BOTANICAL SOCIETY OF EDINBURGH

VOLUME XXXVI.

PART II.

SESSION 1951-52.



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1953

PROCEEDINGS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CXVI

OCTOBER 25, 1951.

Professor Sir WILLIAM WRIGHT SMITH, President, in the Chair.

The following Office-Bearers were elected for Session 1951-52:—

PRESIDENT.

J. M. COWAN, M.A., D.Sc.

VICE-PRESIDENTS.

J. ANTHONY, M.C., M.A., B.Sc. Miss A. M. MACLEOD, Ph.D.	R. A. TAYLOR, Ph.D., D.Sc. Miss M. NOBLE, Ph.D.
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COUNCILLORS.

Sir DONALD POLLOCK, Bart., O.B.E., LL.D., M.D.	J. T. JOHNSTONE, M.A., B.Sc.
W. A. CLARK, B.Sc., Ph.D.	Professor K. W. BRAID, M.A., B.Sc.
G. COCKERHAM, B.Sc., Ph.D.	J. B. SIMPSON, D.Sc.
Mrs. E. M. KNOX, D.Sc.	J. A. MACDONALD, B.Sc., Ph.D., F.R.S.E.
Professor J. R. MATTHEWS, M.A.	P. DAVIS, B.Sc.

Honorary Secretary—J. ROBERTS, B.Sc.

Assistant Secretary—Miss D. E. PURVES.

Cryptogamic Secretary—D. M. HENDERSON, B.Sc.

Treasurer—J. W. H. JOHNSON, C.A.

Artist—R. EUDALL.

Auditor—C. A. SCOTT, C.A.

Editor of "Transactions"—A. M. MACLEOD, Heriot-Watt College, Edinburgh.

Mr. B. L. BURTT and M. CHR. BANGE were elected Ordinary Fellows.

Professor Sir WILLIAM WRIGHT SMITH delivered an address entitled "Instability of Criteria within a Genus."

NOVEMBER 22, 1951.

Mr. J. ANTHONY, Vice-President, in the Chair.

A presentation was made to Dr. MALCOLM WILSON.

Dr. WILSON then read a paper entitled "Evolution of the Uredinales."

DECEMBER 13, 1951.

Dr. J. M. COWAN, President, in the Chair.

Miss B. A. POULTER, Miss M. R. PATON, Mr. W. D. CONNELL, Mr. S. R. CHANT, Mr. M. J. GREEN and Mr. D. W. R. MACKENZIE were elected Ordinary Members.

Mr. J. GRANT ROGER read a paper on "*Diapensia lapponica* in Scotland."

Mr. B. W. RIBBONS, Mr. H. H. DAVIDIAN, Mr. B. L. BURTT and Mr. D. N. HENDERSON read papers on "Other Noteworthy Plants." The papers were illustrated by demonstrations of specimens.

JANUARY 24, 1952.

Dr. J. M. COWAN, President, in the Chair.

Mr. A. CURRIE, Mr. T. CORKE and Mr. D. H. N. SPENCE were elected Ordinary Fellows.

The President referred to the death of Miss D. DRYSDALE and Mr. J. JACK.

Dr. MOWBRAY RITCHIE delivered an address entitled "Chemical Aspects of Photosynthesis."

FEBRUARY 21, 1952.

Dr. J. M. COWAN, President, in the Chair.

Mr. W. D. RICHARDSON and Mr. T. W. SUMMERS were elected Ordinary Fellows.

Mr. B. L. BURTT read a paper entitled "Contacts between Taxonomy and General Botany, with special reference to Studies of Fruits and Seeds."

The following papers were read by title:

1. "The Distribution, Host Range and Seasonal Development of *Puccinia graminis* Pers. in South-East Scotland," by C. C. V. BATTs. (See xxxvi, 48.)
2. "Contribution towards a Fungus Flora of the Small Isles of Inverness," by R. W. G. DENNIS. (See xxxvi, 58.)
3. "Phytoplankton of some Lochs in South Uist and Rhum," by EDNA M. LIND. (See xxxvi, 37.)
4. "Some Scottish Smut Fungi," by MALCOLM WILSON and D. M. HENDERSON. (See xxxvi, 71.)

MARCH 20, 1952.

Dr. J. M. COWAN, President, in the Chair.

Professor I. A. PREECE gave a lecture entitled "Yeast: a Study in Applied Biology."

APRIL 17, 1952.

Mr. J. ANTHONY, Vice-President, in the Chair.

Mr. J. GRANT ROGER read a paper entitled "Flora of Caenlochan, Angus."

The following paper was read by title:

"Flora of Eigg: Additions and Notes," by Mr. D. H. N. SPENCE. (See xxxvi, 74.)

MAY 16, 1952.

Dr. J. M. COWAN, President, in the Chair.

Mr. W. T. HALL gave a lecture on "The Forests of India."

JUNE 19, 1952.

Dr. J. M. COWAN, President, in the Chair.

Miss N. WALDIE and Miss J. B. R. REID were elected Ordinary Fellows.

The following papers were read:

1. "Variation in Species of *Hypericum* L. in Turkey," by Miss B. A. POULTER.
2. "Some Problems in Relation to Germination," by Mr. W. D. CONNELL.
3. "Autolytic and Germinative Changes in the Sugars of Barley," by Mr. D. G. WREAY and Mr. D. C. TRAVIS.
4. "Reaction of *Rhododendron* to *Sporocybe azaleae*," by Mr. S. R. CHANT.

The following paper was read by title:

"A Study of the Vegetative Propagation of Plants, with Special Reference to the Root Initials of *Jasminum nudiflorum* Lindl.," by W. BURNS. (See p. 84.)

The Botanical Society of Edinburgh is greatly indebted to the Carnegie Trust for the Universities of Scotland for a substantial grant towards the publication of this number of the *Transactions*.

EIGHTH INTERNATIONAL BOTANICAL CONGRESS—
PARIS, JULY 1954

SECTION NOMENCLATURE

Proposals regarding the International Code of Botanical Nomenclature (1952) must be submitted to the Rapporteur-Général Dr. J. Lanjouw before 1st December 1953. All proposals can be published in *Taxon*. Botanists preparing proposals are earnestly requested to give them the form of the example which will be published in *Taxon*, vol. 2, no. 2 (March 1953).

Office of the Rapporteur-Général

International Bureau for Plant Taxonomy and Nomenclature,
Lange Nieuwstraat 106, Utrecht, Netherlands.



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TRANSACTIONS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CXVI

REPORT OF THE CRYPTOGAMIC SECTION, 1952.

By D. M. HENDERSON.

A short spring foray was held at Roslin on Saturday, 10th May. Few fungi were collected, the more interesting finds being *Morchella esculenta*, *Milesia kriegeriana* on *Dryopteris dilatata* and *Milesia blechni* on *Blechnum spicant*.

The autumn foray was held in Blairgowrie and district in perfect weather on the 27th, 28th and 29th September. A few collections were made in Glenfarg on the route north.

The banks of the Ericht, visited on the Sunday morning, were bryologically interesting but few fungi were found. As was to be expected from the dryness of the season, the foray to the pine woods round Stormont Loch was much more fruitful. The evening was spent examining specimens in a laboratory made available by Blairgowrie High School. During the evening a short business meeting was held at which the proposed visit of the British Mycological Society to Scotland in 1953 was welcomed.

On Monday, the 29th, Craighall and Bridge of Cally woods were visited; the former yielded a good collection of ferns. In the afternoon a birch wood in Glenshee proved too dry and few collections were made.

Interesting species found were *Sparassis crispa*, *Hygrophorus pustulatus*, *Clitocybe umbonatus* and a small species of *Lentinus* on *Chamaenerion* stems. Dr. R. W. G. Dennis identified the two latter. The nomenclature of the Boleti and Agarics follows Pearson & Dennis' list; the unnecessary quotation of authorities has thus been omitted. Similarly, the nomenclature of the ferns follows Hyde & Dade's *Handbook of Welsh Ferns*. Miss U. K. Duncan kindly supplied the list of the more interesting Bryophytes.

Localities.

1. Glen Farg.	2. Banks of Ericht.	3. Stormont Loch.
4. Craighall.	5. Bleaton Hallet.	6. Bridge of Cally.

FERNS.

CYSTOPTERIS FRAGILIS, 4.
DRYOPTERIS BORRERI, 4; *DILATATA*, 4; *FILIX MAS*
GYMNOCARPIUM DRYOPTERIS, 4.
POLYSTICHUM ACULEATUM, 4; *ANGULARE*, 4.
THELYPTERIS PHEGOPTERIS, 4.

BRYOPHYTES.

SPHAGNUM SQUARROSUM Pers. ex Crome, 3; *SUBSECUNDUM* v. *INUNDATUM* (Russ.) C. Jens, 3; *SUBSECUNDUM* v. *AURICULATUM* (Schp.) Lindb., 3; *FIMBRIATUM* Wils., 3; *GIRGENSOHNII* Russ., 3.
DICRANUM UNDULATUM Ehrh., 3.
BARBULA RUBELLA v. *RUBERRIMA* Ferg., 2.
HYPNUM STRAMINEUM Dicks., 3.
LEPTOGIUM LACERUM f. *FIMBRIATUM* Nyl., 2.

FUNGI.

AMANITA EXCELSA, 5; *MUSCARIA*, 3; *RUBESCENS*, 3.
AMANITOPSIS VAGINATA, 3.
ARMILLARIA MELLEA, 2.
BOLETUS SCABER, 2; *VARIEGATUS*, 3.
CALOCERA VISCOSA, 3.
CLITOCYBE CLAVIPES, 3; *FRAGRANS*, 3; *UMBONATA*, 3.
COLLYBIA MACULATA, 2.
COPRINUS ATRAMENTARIUS, 1, 4; *MICACEUS*, 4.
CORTINARIUS ANOMALUS, 3; *ARMILLATUS*, 3; *CINNAMOMEUS*, 3; *HEMITRICHUS*, 2.
EXIDIA GLANDULOSA, 5.
FISTULINA HEPATICA, 2.
FLAMMULA ALNICOLA, 3; *SAPINEA*, 3.
FOMES ANNOSUS, 2, 6.
GALERA TENERA, 3.
HEBELOMA CRUSTULINEFORME, 4; *MESOPHAEUM*, 6.
HYGROPHORUS PUSTULATUS, 6; *VIRGINEUS*, 6.
HYPHOLOMA SUBLATERITIUM, 2; *FASCICULARE*, 3.
INOCYBE GEOPHYLLA, 4.
LACCARIA AMETHYSTINA, 4; *LACCATA*, 2, 3.
LACTARIUS BLENNIUS, 4; *DELICIOSUS*, 3; *GLYCIOSMUS*, 3, 5; *PLUMBEUS*, 3; *PYROGALUS*, 4; *RUFUS*, 3; *TORMINOSUS*, 3, 2; *VIETUS*, 2.
LENTINUS OMPHALODES var. *TRIDENTINUS* (Sacc. & Syd.) Pilat f. *AURISCALPIUM* Pilat, 4.
LEPIOTA AMIANTHINA, 5.
MARASMIUS ANDROSACEUS, 4; *CONFLUENS*, 2; *DRYOPHILUS*, 2; *RAMEALIS*, 3; *ROTULA*, 3.
MYCENA ALCALINA, 3; *AMMONIACA*, 3; *EPIPTERYGIA*, 4; *GALOPUS*, 4; *INCLINATA*, 4; *POLYGRAMMA*, 4, 5.
NOLANEA STAUROSPORA, 5.
NAUCORIA ESCHAROIDES, 2, 5.

PANAEOLUS CAMPANULATUS, 3, 5.
PAXILLUS INVOLUTUS, 3, 5.
PHALLUS IMPUDICUS, 2.
PHOLIOTA SQUARROSA, 3, 1; MUTABILIS, 4.
PLUTEUS CERVINUS, 3.
POLYPORUS BETULINUS, 3; PERENNIS, 3; SCHWEINITZII, 3; SQUAMOSUS, 3;
STIPTICUS, 4.
POLYSTICTUS ABIETINUS, 3.
PSATHYRELLA GRACILIS, 4.
PSilocybe SEMI-LANCEATA, 5.
RUSSELLA ATROPURPUREA, 3; BRUNNEO-VIOLACEA, 3; CYANOXANTHA, 2;
DELICA, 5, 4, 2; DRIMEIA, 3; EMETICA, 4; FRAGILIS, 3, 2; NIGRICANS, 5;
OCHROLEUCA, 3, 1; VETERNOSA, 3; XERAMPELINA, 3.
SPARASSIS CRISPA, 3.
STROPHARIA AERUGINOSA, 4; SEMI-GLOBATA, 5.
THELEPHORA TERRESTRIS, 3.
TRICHOLOMA FULVUM, 3; RUTILANS, 3; SCULPTURATUM, 3.

A STUDY OF THE VEGETATIVE PROPAGATION OF PLANTS, WITH
SPECIAL REFERENCE TO THE ROOT-INITIALS OF JASMINUM
NUDIFLORUM LINDL.*

By W. BURNS.

(With Plate V.)

(Read by title, 19th June 1952.)

The plant used in this investigation was *Jasminum nudiflorum* Lindl., introduced from North China by Fortune about 1840 (Curtis, 1852). Flowering in Britain takes place from September to May, with the peak months November to January. From March onwards, buds which have not become flowers grow into vegetative shoots. On certain of these branches and at certain times of the year appear root-initials.

The present study is concerned more with the formation of these initials than with their elongation into roots. The work was carried out by an anatomical study of the root-initials and the tissues from which they arise, and by making cuttings of various kinds at various times of the year and growing these in quartz-sand or in water in a cold frame.

THE ROOT-INITIALS.

After July many of the vegetative branches of the current year show small protuberances, typically one on each side of and slightly below the level of a leaf insertion. In section these protuberances are seen to contain one or more root-initials. This accords with the observation of Priestley and Swingle on root-initiation (1929).

A transverse section of the stem of a vegetative branch of the current year (text-fig. 1) shows a well-developed epidermis, two or three layers of cortical tissue containing chlorophyll, further layers of cortex without chlorophyll, followed by a zone of fibrous bundles just outside the phloem, then phloem, cambium and xylem (the last-named formed of closely packed tracheids traversed by numerous medullary rays which broaden out in the phloem; these rays are numerous, practically one ray to every two rows of tracheids).

* A condensed form of this paper was read before Section K of the British Association for the Advancement of Science (Edinburgh, 1951).

There is a large-celled pith. Starch appears in the cortex and the medullary rays, but not in the pith.

Phyllotaxis is opposite and decussate. A transverse section just below a node shows, on two sides, broad leaf-traces. As the leaves are frequently not exactly level with each other, such a section often reveals more of one leaf-trace than the other and may also show part of the axillary bud or bud-trace. Root-initials on the stem normally arise right and left of the broad parenchymatous band belonging to



TEXT-FIG. 1.—Semi-diagrammatic transverse section at level of leaf-insertion in *J. nudiflorum*. Above, in the middle, is the base of the petiole, containing a leaf-trace. Below it is part of the leaf-gap connecting up with the central pith. To right and left are root-initials, inserted in the xylem. Their tips point towards the flanges of the petiole-base.

the leaf-gap which interrupts the central cylinder. Thus there are, at each node, in the "typical" arrangement, four positions where root-initials may appear. Actually none may be produced, or any number from one to four, with initials occasionally twinned (two from the same point of origin).

Root-initials, however, have been found at any point in the margin of the leaf-gap, *e.g.* level with the bud or even behind it (Plate V, *a*). They have also been found in lines leading down from one of the typical nodal positions, apparently following a line of vascular tissue. In addition, root-initials are formed just above the cut at the base of a young cutting, when the cut is in the middle of an

internode. Such initials arise at any point on the circumference, and the roots grow out nearly horizontally. More rarely, root-initials arise in the callus which seals the base of such a cutting, the roots arising from such callus root-initials growing vertically downwards.

The first recognisable sign of a root-initial in a transverse section of *J. nudiflorum* is similar to that described for root-initials in *Coleus* by Smith (1925), *i.e.* a nest of highly meristematic cells with dense protoplasm and large nuclei formed just outside the phloem. Development of such an initial is rapid, the stem tissue being pressed outwards so that, at an early stage, there appears a small protuberance on the smooth green surface of the stem. It would appear, from sections made at various stages, that there is also growth inwards, connecting up the root-initial with the vascular tissue of the central cylinder and burrowing to some extent into it. Sandison (1934), dealing with the formation of root-initials in cuttings of *Lonicera japonica*, remarks: "The greatest degree of organization appears in the pericycle, and, from signs of displacement in the cells of the xylem surrounding the base of the root, it is supposed that organization has proceeded backwards from the pericycle."

Normally, in aerial parts, light and the dryness of the surrounding air arrest the initial before it breaks the surface of the epidermis.

Since the root-initials are seemingly connected in some way with the leaf-traces, attempts were repeatedly made to trace their internal connections. A weak aqueous solution of Magdala Red was supplied to the cut end of the middle leaflet of a leaf, somewhere in the middle of a long leafy cutting of the current year. The lower (cut) end of the cutting was in water. After two or three days one could see the effect of the dye on the whole orthostichy of leaves from the treated leaf to the tip of the cutting. The opposite orthostichy showed no colour. Traces of colour in the orthostichies at right angles to the treated leaf began to appear only near the tip of the cutting. Transverse sections showed that the colour had ascended in one half of the xylem till near the top, whence it seemed to be able to spread to the other half.

This longitudinal division of the stem shows markedly at flowering time. The two flower-buds on opposite sides of a node seldom open together. (In extreme cases one of them may develop into a flower and the other into a vegetative shoot.) This earliness or lateness of flowering may extend up several nodes on one side. It would appear that each leaf is in direct vascular connection with the leaf above and the leaf below it in the same orthostichy, but not

with the leaf opposite (*cf.* Priestley and Scott, 1933). The normal position of the root-initials on the stem corresponds with the point where the leaf-trace impinges on the vascular tissue coming from the leaf above (Plate V. *b*). Beijerinck (1886) had noted this part of the stem as specially likely to produce root-initials; it is reasonable to think that at such a point there may occur a hold-up of substances that affect root-formation.

The occurrence of adventitious roots, far more frequently in the neighbourhood of nodes than at any other point, has been observed by many other writers, *e.g.* Trécul (1846), Priestley and Swingle (1929), Van der Lek (1924), Carlson (1938), Clos (1883) and Worts-mann (1913). Most of these writers suggest that, connected with such an occurrence of root-initials, there is some slowing-up of the current of materials flowing downward from the leaves, this having to do with complications in the course of the transporting channels caused by the leaf-gap. There is a certain amount of indirect evidence in the same sense, since, in many plants, including *J. nudiflorum*, artificial bending of the stem has the effect of inducing the formation of root-initials at the bend, presumably owing to the hold-up of root-forming substances from the leaves.

That *J. nudiflorum* produces such substances in excess, particularly during July and August, has been repeatedly shown in these and other experiments reported here. Not only does a fragment of a leaf (*e.g.* a single middle leaflet) have the power to produce roots in the stem portion attached to it, but if, during the main rooting season, the basal callus and roots are cut off from a rooted cutting, a second callus and a new crop of roots are quickly formed, provided the leaves on the cutting are intact and healthy.

Root-initials may occur on any branch, thick or thin. The short side-branches formed at the end of the summer, which bear the first flowers of the following winter, carry very few root-initials, but it is possible to find a cutting, made from such a branch, planted just before flowering time, producing a flower with a root arising just beneath it.

EXPERIMENTS ON CUTTINGS.

The vegetative shoot of *J. nudiflorum* (text-fig. 2, *a*), which starts its growth in the end of March, normally produces certain very small closely packed bud-scales (which may later develop adventitious buds in their axils if the main bud is lost), two prophylls, a node with simple sessile leaves, one or two nodes with simple stalked

leaves, and thereafter nodes with normal trifoliate leaves. The green square stem carries slight flanges running down part of the



TEXT-FIG. 2a.—Young vegetative shoot of *J. nudiflorum*, arising as the development of a non-flowering bud of a shoot of the previous year.

TEXT-FIG. 2b.—Diagram to show points of origin of adventitious roots on a summer cutting of *J. nudiflorum*, grown in a cool frame with a fairly moist atmosphere.

way into each internode from each leaf. When young the branches protrude at all angles, but, when old, seem to droop, producing a weeping habit. This does not apply to the short branches which

bear the first flowers. Cuttings in these experiments were usually made from strong vegetative branches, and such cuttings may be discussed under a number of different headings:—

(1) *Early summer cuttings of the current year's growth.*

A cutting of about 8 cm. long (the whole branch), made in late May or early June, produces basal callus and from three to eight roots from the stem just above this callus. There are no aerial root-initials at this stage. Even younger shoots can root. On two occasions small adventitious shoots of only 2 cm. long have been accidentally rubbed off branches of the previous year's wood and have fallen on the sand, where they rooted.

As noted by Swartley (1943), in the allied genus *Forsythia*, root-initials can be seen even in the resting buds, and even leaves are able to root. Trials of the rooting of leaves of *J. nudiflorum*, made in the present investigation, gave callus every time, and a root on several occasions.

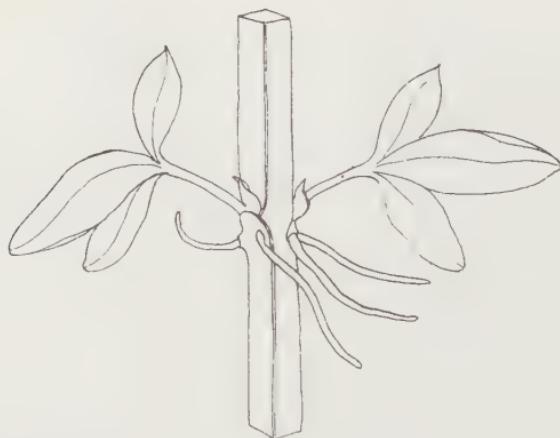
(2) *Later summer cuttings of the current year's growth.*

In these, in addition to basal callus and its associated roots, there are visible root-initials higher up the stem. As already mentioned, these show up as little bulges to right and left of, and slightly below, the level of a leaf-insertion. If a transparent glass jar is placed over the cutting while it is in the sand, the appearance of these root-initials can be speeded up by as much as a fortnight, and they also break surface and grow in the saturated atmosphere (text-fig. 2, b). Those near the sand grow into it, making excellent small-scale models of stilt-roots.

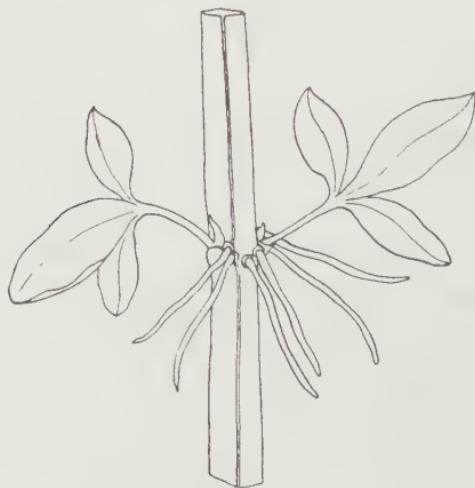
Van der Lek (1924), dealing with *Salix*, remarks that one-year-old cuttings, placed with their bases in water and their upper parts in a damp chamber, quickly (in most species, but not in all) formed roots over the whole cutting. Bouillenne and Went (1933), working in Buitenzorg (Java), found that, in the rainy season, *Acalypha Wilkesiana* var. *triumphans* produced so many roots (in nature) along its stems that it was impossible to get a piece without root-initials to use as a control.

There is one curious and probably significant fact about the position of root-initials in the aerial parts of current year's cuttings grown in a saturated atmosphere. They tend to appear, not at the "typical" position (text-fig. 3; Plate V, b), but higher up, i.e. level with the leaf base (often in the recess between the petiole flange

and the stem), and even behind the bud (text-fig. 4; Plate V, *a*). The same phenomenon is noticeable in roots produced at the nodes of stems grown inverted in water, the submerged parts (especially

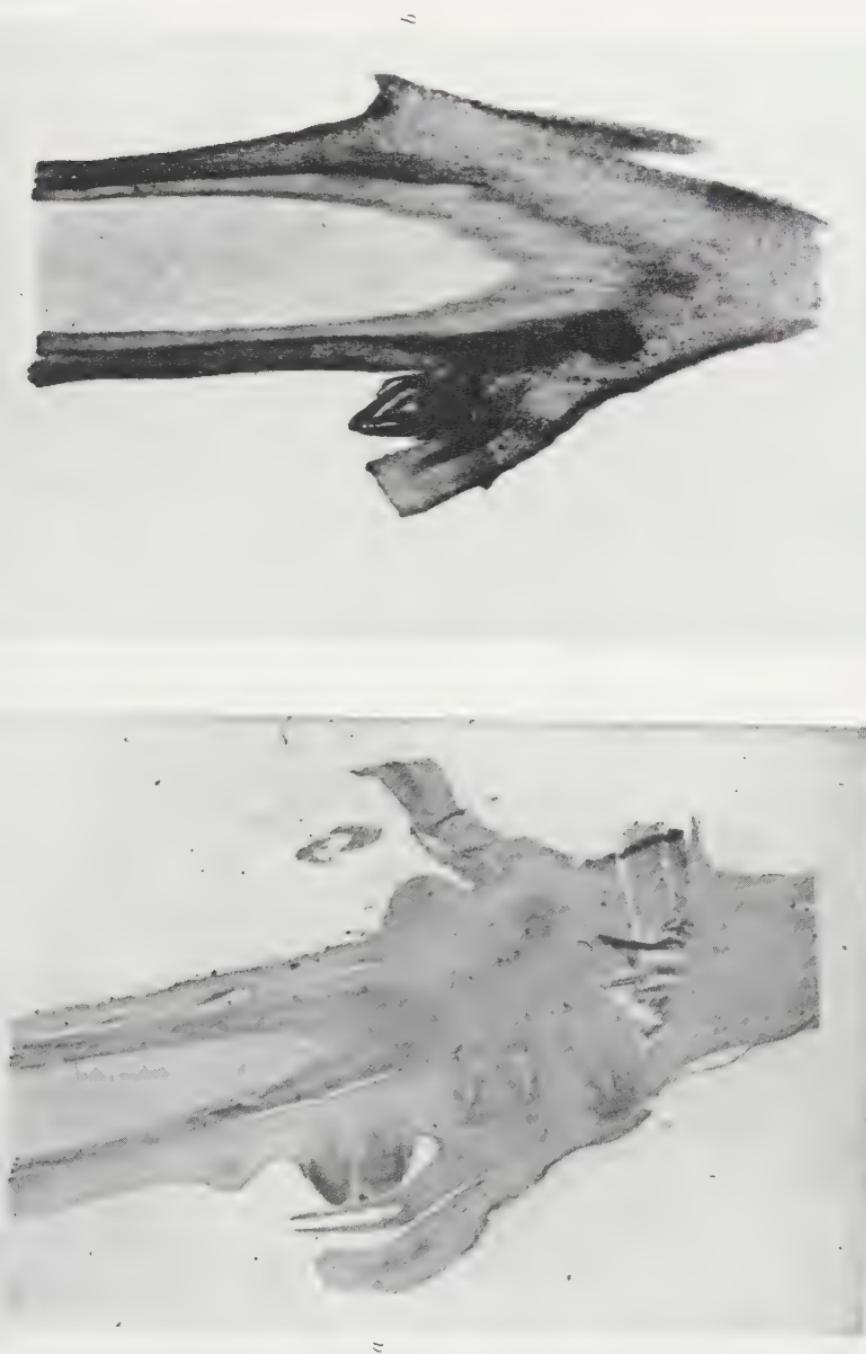


TEXT-FIG. 3.—Normal position of adventitious roots at a node of *J. nudiflorum*.



TEXT-FIG. 4.—Position of adventitious roots at a node of *J. nudiflorum* when grown in a saturated atmosphere or as a cutting inverted in water or a solution of indole-acetic acid.

if submerged in a 20 p.p.m. solution of indole acetic acid) producing roots at the nodes in the positions just described. If, as seems quite possible, the sap-currents in the cutting are markedly slowed up by saturation or by inversion plus immersion, then it would be reasonable to expect the hold-up of root-forming materials from the leaf above to occur higher up the stem and to produce its effects



"a, Longitudinal section through a node of a cutting of *J. nudiformis* grown inverted in a solution of indole-acetic acid. On the left are visible the base of the petiole and the bud. Behind the bud are two well-marked root-initials. Below it are three others.

"b, Longitudinal section through a node of *J. nudiformis*. To the left is the base of the petiole, showing a part of the leaf-trace. Next to it is the bud. There is a dark line of vascular tissue coming from above, passing the bud and lower

earlier, in the higher part of the fork of the vascular tissue at the leaf-gap.

There is one significant fact about the point of first appearance of root-initials. The highest point where nodal root-initials appear is where the light green of the actively growing terminal portion is changing to the deeper green of the part where growth in length is slowing down. There is a similar happening if a dormant terminal bud is awakened by keeping a cutting in a warm damp house in winter. Root-initials then form on the older part just below the new growth, and finally begin to form on the new growth itself.

There are observations by other workers that, in other plants, at the point in a stem where, in the Jasmine, root-initials first appear, there is a sudden rise in the concentration of auxin. Hatcher (1947), dealing with apple and plum stocks, remarks: "At the actively growing tip the auxin value is moderately high, falling to a much lower level in the young expanding internodes, and rising to a second peak in the internodes immediately below these." A similar observation was reported by Avery, Burkholder and Creighton (1937) for *Aesculus* and *Malus*.

Repeated experiments carried out on *J. nudiflorum* by the present author show that, if long sucker-like branches are cut out into serial parts (of five or six nodes each at the top and three or four nodes each at the base), and these are planted, then rooting capacity is highest in the top section and falls off progressively towards the lower parts, which may not root at all, though they do form callus.

(3) *Autumn cuttings of single nodes with varying amounts of leaf, also cuttings of leafless internodes.*

A single adult node with its two fully-formed leaves, used as a cutting in July or August, can and usually does produce a callus and a great crop of roots. If only one leaf is left on, then the roots will usually (but not always) be on that side of the stem fragment below. If both leaves have been removed, there are no roots, but it requires only a small amount of lamina to cause their appearance.

Cuttings from leafless internodes never root, though they generally form a basal callus. Molisch (1935), working mainly with *Ampelopsis quinquefolia*, found the same lack of rooting in budless internodes.

Some single-node cuttings with two leaves may for a time produce no roots but only a large callus. Cutting off this callus and re-planting usually induces rooting.

If there is practically no internode below the leaf or leaves in a single-node cutting (*i.e.* just enough stem left to hold the leaves together), then rooting is, as a rule, copious. If, on the other hand, the whole length of the internode is left below the leaves and the base of this internode planted shallowly in the sand, rooting often does not follow. If such a non-rooting cutting is then either buried up to the leaves or if the lower internodal part is cut off up to the level of the leaves, then rooting results. This would appear to indicate that something essential for rooting, produced by the leaves, is inhibited or destroyed in the exposed internode. Chouard (1948-49) notes the more or less rapid destruction of auxins by oxidation in the stem.

(4) *Autumn cuttings allowed to overwinter until the following spring or summer.*

Cuttings of several internodes in length, taken late in the year (September or October), usually drop their leaves in the frame. In late autumn cuttings some of the buds may turn into flowers, others may remain dormant till the following spring, if the cutting survives, and it is amazing how many cuttings do survive even without roots. The behaviour of such cuttings is very variable; two illustrative examples are quoted:

CASE 1.—Strong leafy branch of 20 nodes cut into 6 serial sections (numbered from the top); planted in cold frame, 14th September 1950.

Section.	1.	2.	3.	4.	5.	6.
1950. Oct. 20	Callus; roots from node above cut.	Like 1.	Like 1, also root from tumour higher up.	Callus; one root.	Callus; no roots.	Like 5.

(Callus and roots removed; sections replanted)

1951. Jan. 3	Leaves retained; callus; 7 roots (3 to 10 cm.).	One leaf; 3 buds starting; callus; 9 roots (3 to 18 cm.).	One leaf; 4 buds starting; callus; 10 roots (12 to 21 cm.).	No leaves; callus; 5 roots (1 to 8 cm.).	No leaves, callus or roots.	Like 5.
Apr. 6	Nos. 1 to 4 had axillary shoots (3 to 8 cm.); longer but no new roots.				Dead.	Dead.

Time 209 days.

CASE 2.—Another branch in 8 sections; planted in cold frame, 4th October 1950.

Sections 1 to 3 produced callus by 25th October and roots by 24th November. Sections 5 to 8 produced callus only. Only section 4 was retained. This was leafless, healthy and with a callus, but no roots, on 24th November 1950. This callus continued to grow and broaden, and changed from yellow to brown. Axillary bud-shoots were 1 cm. long on 29th June 1951. The callus was then removed. By 29th August 1951 the callus was faintly reorganised, the axillary shoots were about 6 cm. long and there were 5 roots (1 to 2.2 cm.) arising from the third node from the top.

Time 331 days.

(5) *Cuttings with "heels" (i.e. a branch of the current year with a portion of the year before, or of the two years before, attached).*

Such cuttings, whether kept in sand or in water, usually showed aerial rooting from the current year's growth, followed by rooting of the "heel" as if the rooting stimulus had begun in the current year's growth and travelled downwards. Occasionally the "heel" showed one or two roots earlier than the current year's growth, but in that case the growth of the current year was elongating rapidly and it is more than probable that a stimulus from the growing portion travelled down to the stump of the previous year and started into growth concealed root-initials already formed there. In one "heeled" cutting there were two branches of the current year on a last year's "heel". The heel and *one* of the current year's branches rooted, the other branch of the current year did not. This was one node higher up on the old branch than the other, but there was no obvious reason for the difference in rooting. This is only one of many indications that rooting or non-rooting is determined by a large number of factors acting together locally.

So far as horticultural practice is concerned, there is, in *Jasminum nudiflorum*, no advantage in the planting of a "heeled" cutting against a "non-heeled" one of the current year.

USE OF INDOLE ACETIC ACID.

A few experiments were undertaken to compare the behaviour of current year's cuttings when kept in water and in solutions of indole acetic acid. The cuttings were either erect or inverted. The two strengths of indole acetic acid solution used (20 and 50 parts per million) gave identical results.

In erect cuttings the only effect of the indole acetic acid was an acceleration and increase of rooting. In the inverted cuttings, however, the growing-point turned up sharply and quickly, growing

up parallel to the descending part of the cutting, and with a sharp bend in the submerged part. There was a burst of roots from this sharply curved part, and copious rooting from the nodes immediately (morphologically) below. These roots were in the position already mentioned in connection with root formation in saturated atmospheres, *i.e.* level with or behind the bud.

Loeb (1917) has shown that in *Bryophyllum calycinum* the leaf (in addition to inducing root formation) has also an accelerating effect upon the geotropic curvature of the horizontally placed stem. The accumulation of growth substance on the lower side of any organ has been reported by many workers, *e.g.* Söding (1938). This effect, as well as rooting, appears to be reinforced, in *J. nudiflorum*, by indole acetic acid. In control experiments, the growing tip did finally turn upwards, but much more slowly than in the treated jars and with much less new tip tissue.

An extraordinary effect was produced by indole acetic acid on a stout cutting taken from a strong branch on 7th October 1938. This cutting had two branches from its upper node, carrying leaves. The lower part of the cutting was in 50 p.p.m. indole acetic acid. On 3rd December, when it was transferred from the cold frame to a house at 65° F., many of the leaves had dried and fallen, though the tips of the branches were alive. Later there was a further burst of growth from the young tips, but the young leaves afterwards died. At the base of the cutting, however (12th January), there had developed a tumour which split, showing a great number of young roots inside, and there were also many roots from the internode and node above.

A somewhat similar phenomenon was reported by Zimmerman and Hitchcock (1935) when a tobacco plant growing in soil treated with indole acetic acid thickened up, burst and showed thousands of small roots inside the stem.

DISCUSSION.

It would appear that the leaf is a powerful organ for the initiation of root-initials. In its absence there is, in the current year's shoot, no appearance of these, and internodes of the current year by themselves never root. Nor do root-initials normally appear on the stem until that portion is reached where the internodes are ceasing to elongate and the leaves are adult. It has been indicated by other workers that, at this point in the stem of other species, there is the highest concentration of auxin. From that point downwards, root-

initials may appear in the position previously described. There may be some correlation between the occurrence of initials and the point where the vascular tissues coming from a leaf higher up coalesce with those of the trace coming from the leaf immediately below in the same orthostichy. This certainly is the case in *J. nudiflorum*. This junction and the diversion of vascular tissue caused by the leaf-gap have frequently been regarded as having the effect of holding up or slowing the stream of substances (including root-forming substances) from the leaf or leaves above and so conduced to the appearance of root-initials where, in fact, they do normally occur.

An interesting exception is seen in stems grown in saturated air, or inverted and submerged. There the root-initials occur higher up on the leaf-gap fringe, level with or even behind the leaf insertion. The slowing up or practical stoppage of the internal current in such cases is regarded as a possible explanation, and this may also be the reason for the remarkable outburst of aerial rooting in tropical forests during the rainy season.

On various occasions root-initials have been found to follow for a shorter or longer distance the lines of vascular tissue, again indicating the connection of such tissue with root production.

In normal circumstances, in *J. nudiflorum*, only certain nodes and certain angles of these nodes produce root-initials, and often root-initials may be missing altogether. This would seem to indicate (as has been emphasised by Chouard, 1948-49) that root-initiation is influenced by a complex of factors and that the absence or insufficiency of one of these is enough to prevent appearance of root-initials.

On cuttings, even single-node cuttings, taken before there is any sign of leaf-abscission, the time of greatest root-initiating activity in *J. nudiflorum* is during July, August and September. If cuttings are taken at this time with a full crop of healthy leaves and kept in a cold frame they may retain some of these leaves (especially the younger ones) for a very long time and go on producing roots till the end of December. Branches remaining on the tree are by that time leafless and flowering.

Cuttings taken later than October and placed in the cold frame will not, as a rule, root till the following April, if they survive so long.

Late summer cuttings may be amazingly long-lived even without roots. This may be due to their large store of food materials in the form of obvious starch, probably also sugars, and to the mild assimilative powers of the chlorophyll tissue of the cortex. This is,

of course, provided water-loss is reduced, as happens in the cold frame.

Root-forming power is least in the basal sections of a current year's shoot and greatest in the top sections.

Root-Forming Substances.

That auxin is one substance determining the formation of root-initials is now a general belief, though, as Chouard (1948-49) remarks, auxin is to be regarded more as a revealer of existing root-forming potentialities than as a root-producer. This remark is based on observations by himself, by Fisch nich (1938), by Stoughton and Plant (1938) and by others, that varying doses of growth substance (heteroauxin) produce, from undifferentiated tissue, buds, roots or tumours according to the increasing strength of the dose.*

Where tissue is already differentiated, as in plant stems, certain of the deep-lying tissues may (according to one viewpoint) contain, from their embryonic stages, a substance which determines that roots shall arise there when the appropriate stimuli are applied.

This is one of the aspects of the rhizocaline theory, originated by Bouillenne and Went (1933), though the idea of specific organ-forming substances had been put forward by Sachs, apparently on purely speculative grounds, as early as 1880, and Sachs himself attributed the germ of the idea to that early French experimenter Duhamel (1758).

The rhizocaline theory has been elaborated in detail and with enthusiasm by Bouillenne and his associates, and according to them this substance (originating from the leaves) exists in the plant in both fixed and mobile forms.

Rhizocaline, however, has not been isolated as (for example) auxin has, and remains hypothetical.

The experiments reported in this paper cannot be said to give evidence either for or against the rhizocaline theory, since it is

* The following passage (freely translated) from Chouard briefly gives his point of view: "Let us avoid extreme and excessive opinions. We do not say 'Auxin is rhizocaline'; we do not say 'Auxin has nothing to do with root-initiation'; we say 'Root initiation implies complex factors to which we give the short name of rhizocaline'." (Incidentally, this is *not* Bouillenne's definition of rhizocaline.—Author.) "Among these factors there is probably a specific hormone, as the experiments of Bouillenne indicate. There are probably factors located in the tissues. There is certainly auxin, which is a complementary factor but powerful to reveal root-forming potentialities. Auxin is a revealer, very active and often necessary, of the most diverse morphogenic aptitudes. But it is a differential revealer. Its optimum concentration to reveal stem-forming potentialities is small, that which reveals root-forming potentialities is greater; that which reveals a potentiality to form tumours is greater still (for the same species)."

difficult to disentangle possible hormone effects from those of nutrition.

There must also be taken into account the effects of wounding (claimed by some to be due to a wound hormone) and the still more formidable effect of removing a branch from its place in the parent system.

Finally, the root is the instrument whereby the sporophyte achieved an independent land existence. Bower (1908) suggests that there is no sufficient or decisive evidence as to how the root came into existence in Vascular Plants, but he inclines to the view that the root arose as a new type of haustorial outgrowth not originally of shoot nature. He remarks: "An analysis of even the most complex types of the vegetative system in Vascular Plants involves only the factors thus disclosed, *i.e.* the shoot consisting of axis and leaves, with occasional emergences or hairs and the accessory roots. The apical growth of the shoot may be continued indefinitely with indefinite repetition of its several appendages, or it may itself be duplicated by terminal or lateral branchings, with or without accessory roots."

One is led to the conclusion that presence of adventitious roots is a primitive phenomenon which may persist in certain plants with creeping stems and in *Jasminum nudiflorum*, whose hanging branches are tending in that direction and do, in fact, root where they touch the ground, and that in many plants such adventitious rooting can be re-awakened by cuttings, marcottes or layers.

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THE GENUS TRICHODERMA: ITS RELATIONSHIP WITH *ARMILLARIA MELLEA* (VAHL EX FRIES) QUEL. AND *POLYPORUS SCHWEINITZII* FR., TOGETHER WITH PRELIMINARY OBSERVATIONS ON ITS ECOLOGY IN WOODLAND SOILS.

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(With Plate VI.)

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INTRODUCTION.

The genus *Trichoderma*, first described by Persoon (1794), was recognised as being a part of the soil micro-flora as a result of the investigations of Oudemans and Koning (1902). During the next three decades it was isolated from soils all over the world, and it became apparent that it was one of the commonest genera of fungi in the majority of soils. During this period, taxonomists tended to consider the existence of several distinct species within the genus. Also, at this time, considerable work was carried out on the bio-chemistry of soil fungi in general, and *Trichoderma* was shown to be a powerful decomposer of cellulose (Blumer, 1944); Waksman (1927, 1944) demonstrated that it was capable of liberating ammonia from protein material, though capable of only limited lignin decomposition. More recent taxonomic work on the genus tends to discredit many of the species described by earlier workers, and Gilman (1945) recognises only four species, while Bisby (1939) considers the genus to be monotypic.

Interest in the genus was further stimulated by Weindling (1932), who showed that *Trichoderma lignorum* (Tode) Harz could parasitise other soil fungi. Vuillemin in 1887 had illustrated hyphae of *T. viride* Pers. ex Fries attacking a hypha of *Mucor*, but this early evidence of its parasitism seems to have been overlooked by subsequent investigators. Since 1932, Brian (1944), Brian and Hemming (1945), Brian and McGowan (1945), Brian *et al.* (1946) and Weindling (1934 and 1941) have isolated and studied toxins produced by species of *Trichoderma*. Comparatively little work has been done with the object of determining whether other soil fungi are

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parasitised by *Trichoderma*, and few investigations have been published on its quantitative ecology. Graham (1948) has shown that *Trichoderma* is parasitic to *Fomes annosus* (Fr.) Cooke, while Bliss (1941) states that the growth of *Armillaria mellea* is inhibited in culture by *T. lignorum* but that it is not destroyed in wood after the formation of the pseudosclerotium.

In addition, the genus *Trichoderma* has been shown by Graham (1948), Weindling (1932), Waksman (1945) and Rishbeth (1950), to be capable, through its powers of parasitising certain other fungi, of exerting a considerable influence on organisms in the soil, and it was therefore considered that information of value might be forthcoming from a study of its quantitative distribution in various soils. Many workers—a comprehensive list is given by Gilman (1945)—have reported the isolation of species of *Trichoderma* from soils of various types in many different countries, but these reports have been essentially qualitative in nature and have given little indication of the quantity of the fungus present. Furthermore, the descriptions of the soils from which isolations were made are, with few exceptions (Okada, 1938, and Rishbeth, 1950, 1951), rather vague. Details of pH, parent rocks, type of drainage and nature of higher plants forming the surface communities have in the main been omitted.

The present preliminary series of observations is concerned primarily with the distribution of *Trichoderma* in woodland soils. Opinion is divided on the occurrence of *Trichoderma* in such a habitat. Morrow (1932) failed to isolate the fungus from pine forest soils with pH values between 5.75 and 6.36, and Paine (1927) obtained a positive result in only two out of eight samples taken from virgin timberland. On the other hand, Jensen (1931) isolated *Trichoderma* species from eleven out of fifteen forest soils which he examined, as against only two out of eighteen field soils. He estimated that it usually formed less than 10 per cent. of the total fungal population. Okada (1938) found the fungus to be abundant in Fagetum, Abietetum and Pinetum on Mt. Hakkoda; the only soil from which he failed to isolate it was sandy, with a pH value 2.0–2.2. Rathbun (1914) found *Trichoderma koningi* Oudemans to be the most abundant species in pine seed-beds, and Waksman (1944) states that forest, moor and heath soils in Denmark contain a characteristic *Trichoderma* flora. More recently, Rishbeth (1951 a), in the latest of his series of papers on *Fomes annosus*, finds *Trichoderma* to be frequent in acid woodland soils, but much less so in alkaline.

In view of these facts it was decided to investigate more fully the relationship between *Trichoderma* and *Armillaria mellea* and to

determine if any parasitic action is discernible towards *Polyporus schweinitzii*, another important wood-rotting fungus which can exist in the soil. An attempt was also made to study the quantitative distribution of *Trichoderma* in woodland soils.

PART I.

PARASITISM OF FUNGI BY TRICHODERMA IN CULTURE.

Materials and Methods.

The *Trichoderma* material for this study was obtained mainly by isolation from soils in and around Edinburgh. Ten isolates in all were chosen: one was from a laboratory stock culture, one was isolated from inside a stem of *Rubus fruticosus*, and the remainder were isolated direct from the soil. Gilman (1945) would call two of these isolates *T. koningi* Oudemans and the remainder *T. lignorum* (Tode) Harz. Bisby (1939), however, would include them all in *T. viride* Pers. ex Fries.

Two strains of *Armillaria mellea* were used, both obtained from the Department of Scientific and Industrial Research, Princes Risborough. Rhizomorphs were freely produced by both strains on malt agar. The culture of *Polyporus schweinitzii* was also obtained from Princes Risborough, having originally been isolated from infected wood. Chlamydospores were freely produced in culture.

The parasitism of *Trichoderma* on these two fungi was most suitably tested by growing them on parallel, hanging agar smears in van Tieghem cells in a Petri dish. The cells were first sterilised in the Petri dishes and, with a fine pipette, two small parallel smears of malt agar were placed on the cover-glass of each cell, which was subsequently inverted. As *Trichoderma* grew more rapidly than either *A. mellea* or *P. schweinitzii*, one of the latter was inoculated first on to one of the smears and incubated for a few days until the colony had reached a convenient size, whereupon the second smear was inoculated with the required *Trichoderma* strain. A moist atmosphere was maintained by placing a filter paper moistened with sterile water, and with circles removed to accommodate the glass rings of the cells, at the base of the Petri dish. The cultures were examined repeatedly under high or low power and, with care, oil immersion objectives could be used, with the minimum chance of atmospheric contamination.

It has been shown by Weindling (1934, 1941) that the stability of the toxins produced by strains of *Trichoderma* varies with the pH of the environment. The parasitism of *Trichoderma* on the two hosts was therefore tested in media of different pH values. All ten isolates of *Trichoderma* were opposed in turn to the two strains of *A. mellea* and to *P. schweinitzii*, on media having pH values 3·4, 5·1, 7·0. Control cells in which both smears were inoculated with an isolate of *Trichoderma* or with a strain of *A. mellea* or with *P. schweinitzii* were also set up. In this way it was possible to check that any disintegration seen in the opposed cultures was not due to the drying up or exhaustion of the agar smears. Provided a humid atmosphere was maintained around the van Tieghem cells in the Petri dishes, no deterioration of the hyphae due to exhaustion of the medium could be observed in the control cells for at least seven days after inoculation. No observations on parasitism were made later than seven days after both smears had been inoculated.

Parasitism of Trichoderma on Armillaria mellea.

All the isolates of *Trichoderma* examined were parasitic to *A. mellea* to a degree which, as will be shown, varied with the pH value of the medium and with the position at which the respective hyphae came into contact with one another.

When the two fungi were opposed on a medium of pH 3·4, the *Trichoderma* colony invaded that of *Armillaria*. When the meeting took place on the agar, growth of the latter fungus appeared to stop almost immediately in the region of the invasion. The *Trichoderma* hyphae continued to grow and were stimulated into branching by this proximity, the branches, growing along the host hypha, maintaining close contact with it (Plate VI, 1 and 2). Coiling round, and penetration of the host hypha could be seen, though only infrequently (Plate VI, 2 and 3). After the *Armillaria* hyphae had been in contact with those of *Trichoderma* for a considerable period (24 hours), they began to show signs of disintegration (Plate VI, 4), of vacuolation of the protoplasm, and later collapse of the hyphal wall. Groups of crystals and breaking of the host hyphae at the septa, as observed by Weindling (1932), were not detected. The host hyphae not in actual contact with the *Trichoderma* hyphae showed signs of disintegration only after a much longer period (3 days), and disintegration did not appear to be so complete. Repeated attempts to subculture *A. mellea*, after the entire colony had been invaded, were unsuccessful, the colony apparently having been killed outright.

When the two fungi were opposed on a medium of pH 5·1, parasitism by *Trichoderma* was again clearly evident but it appeared to be less severe than on the more acid medium. Growth of the *Armillaria* colony in the region of invasion stopped almost immediately, though penetration was not observed. The *Trichoderma* hyphae grew closely alongside, touching those of *Armillaria* as before, but a proportion of the latter did not appear to show signs of disintegration even after an interval of three or four days. Those hyphae close to, but not actually touching, the *Trichoderma* hyphae showed no signs of disintegration. Attempts to subculture the *Armillaria* after the invasion of the whole colony met with very limited success, and, seven days after the invasion, only two of the twenty colonies could be shown to be alive.

When the two fungi were opposed on a medium of pH 7·0, parasitism was not observed. The two colonies came together and growth of both continued apparently unhindered. *Trichoderma* hyphae did not grow alongside those of the host, although stimulation of the *Trichoderma* to branch could occasionally be observed when the two mycelia crossed. More than half of the *Armillaria* colonies were successfully subcultured seven days after the invasion had taken place.

When the two colonies met on the glass between the smears of agar, the *Armillaria* hyphae at the point of invasion continued to grow for some considerable time. The *Trichoderma* hyphae were stimulated into branching when they touched those of the host. The host hyphae, in contact with those of *Trichoderma*, showed signs of disintegration slightly sooner than was the case when they were in contact on the medium. The hyphae of *Armillaria* which were near but not touching those of *Trichoderma* showed no signs of deterioration, even after a period of several days. The acidity of the medium did not appear to influence the degree of parasitism observable on the glass.

The production of conidia by *Trichoderma* was stimulated by the proximity of the host. When cultures of *A. mellea*, producing rhizomorphs on malt agar at pH 3·4, were inoculated with *Trichoderma* near the growing tips, growth of the rhizomorphs stopped after about two days and dense masses of conidia appeared, closely invested by *Trichoderma* hyphae. Four days after the rhizomorphs had stopped growing, 1 cm. lengths were cut from the tips, removed from the culture, scraped free of the investing mycelium and conidia, washed in sterile water, dipped in 50 per cent. alcohol for a few seconds and washed again in sterile water. After this treatment

more than half of them grew when placed on fresh medium. When rhizomorphs which had not been in contact with *Trichoderma* were subjected to the same treatment, approximately the same proportion was found to continue growth. This suggests that *Trichoderma* has little or no effect on the rhizomorphs, consisting as they do of material homologous to the pseudosclerotium.

Parasitism of Polyporus schweinitzii.

When *Trichoderma* was opposed to *P. schweinitzii* on a medium of pH 3.4, the host colony was invaded. Hyphae of *Trichoderma* on encountering the hyphae of the host frequently, though not invariably, grew alongside them, though the contact was not so close as that observed with *Armillaria*. Coiling of the *Trichoderma* hyphae around those of *P. schweinitzii* took place infrequently, and penetration of the host hyphae was never observed. Those which were actually touching the *Trichoderma* hyphae deteriorated after about two days to a limited extent only, accompanied, in some parts of the culture, by a slight browning of the deteriorating hyphae. On one occasion only did crystals similar to those described by Weindling (1932) and by Graham (1948) appear in the region of deterioration. *P. schweinitzii*, when grown on malt agar, forms large numbers of chlamydospores, whose formation does not appear to be influenced to any great extent by the acidity of the medium. When formed on the medium these chlamydospores did not appear to be attacked by the *Trichoderma* hyphae.

When the two fungi were opposed on media having pH 5.1 and 7.0, only very slight parasitism was observed. Attempts were made to subculture *P. schweinitzii* as long as possible after the invasion of the colony but before the medium was exhausted. This was successfully achieved with mycelium growing on media at all three pH values, but as it was difficult to avoid transferring some of the chlamydospores to the subculture, this evidence must be regarded as inconclusive.

Hyphae of *P. schweinitzii* on the glass between the smears showed little deterioration even when in close contact with those of *Trichoderma*. Chlamydospores formed on the glass, however, were frequently closely enveloped by *Trichoderma* hyphae (Plate VI, 5 and 6), although the latter seemed to be incapable of causing any visible deterioration however long they were in contact with the spores. On one occasion a chlamydospore closely invested by *Trichoderma* hyphae was observed to form a short germ tube.

In contrast to *Armillaria*, the proximity of *P. schweinitzii* did not seem to stimulate any increased formation of conidia by *Trichoderma*.

DISCUSSION.

Observations of fungi isolated from their normal environment and under artificial conditions are useful, but they must be interpreted with caution. It is obviously impossible to say that because two fungi react in a certain way towards each other on malt agar, they will necessarily behave in the same way when surrounded in the soil by the vast assemblage of other microbiota.

It is clear that both *A. mellea* and *P. schweinitzii* are parasitised by *Trichoderma* under certain conditions and they must therefore be added to its ever-growing list of hosts. Both these hosts appear to be more resistant to *Trichoderma* than are *Rhizoctonia solani* Kühn (see Windling, 1932) or *Fomes annosus* (see Rishbeth, 1950). The long-range effects mentioned by these authors were not discernible in the present investigation, and the disintegration of the hyphae of *A. mellea* and *P. schweinitzii* was much less sudden than that described. It does seem possible, however, that *Trichoderma* may exert some controlling influence on the hyphae of *A. mellea* in more acid soils. Rhizomorphs are probably little affected, except perhaps in their rate of growth, which may be somewhat reduced. It is difficult to see how the presence of *Trichoderma* could have any influence on *Armillaria* in neutral or alkaline soils, and as soils having a pH value as low as 3.4 are comparatively rare in nature, it seems unlikely that *Trichoderma* can ever have a great influence on the growth of *P. schweinitzii* in the soil.

PART II.

ECOLOGY OF TRICHODERMA IN WOODLAND SOIL.

Materials and Method.

To facilitate the estimation of *Trichoderma* in various soil samples, an attempt was made to evolve a selective medium capable of inhibiting the growth of as many types of organisms as possible while at the same time allowing *Trichoderma* to grow freely. Since *Trichoderma* grows well on 2½ per cent. malt agar, this was chosen as the basis of the medium. In order to inhibit the growth of the majority of bacteria, the medium was adjusted to pH 3.0-3.2, at which all *Trichoderma* strains grew well. Series of Petri dishes

were prepared containing the acidified medium to which had been added varying amounts of the substances whose selective properties were being investigated. All ten isolates of *Trichoderma*, both as mycelium and as conidia, were used to inoculate each concentration of the substance under investigation. The criterion of tolerance was taken to be the production of a colony of at least 5 mm. in diameter after incubation at 23° C. for seven days.

Of all the substances tested, picric acid showed the most promise, all strains of *Trichoderma* being able to tolerate a medium containing 0.1 per cent., at which concentration the growth of many other soil fungi was inhibited. Organisms capable of growth on this acidified malt agar—picric acid medium included many species of *Penicillium*, *Aspergillus niger* Tieghem, and certain unidentified yeasts, whereas *Cephalosporium* and many of the *Aspergillaceae* and *Mucoraceae* appeared to be entirely inhibited. In view of this toleration shown by *Trichoderma* towards picric acid, the resistance of the mycelium and conidia respectively to a saturated aqueous solution of picric acid were tested, with a view to finding whether pre-treatment of a soil sample with picric acid solution would achieve the same results as a selective medium.

The method used has already been described (Aytoun, 1951). It was found that conidia which had been soaked in a saturated aqueous solution of picric acid for seventy-two hours were capable of germination; after soaking for seven days, however, no germination could be observed. Conidia which had been soaked in distilled water for twenty-eight days germinated readily. Mycelium which had been soaked for one minute in the picric acid solution was still capable of continuing growth. Two minutes soaking killed it, whereas it survived soaking in distilled water for eight days. All ten isolates of *Trichoderma* showed the same powers of resistance to picric acid; prior to dilution, soil samples were therefore treated for thirty seconds with the picric acid solution, as described below.

Sampling and Counting Methods.

All soil samples were taken at a depth of 10 cm. A small furrow, with clean-cut edges, approximately 40 cm. long, 15 cm. deep and 15 cm. wide was dug by means of a sterile trowel. A sterile test-tube was then pushed into the side of the furrow to a depth of about 4 cm. and withdrawn, bringing with it a core of soil which was pushed down into the tube and broken up with a sterile spatula. This was repeated, until a sample consisting of about 10 g. of soil

was obtained. Two lots of four samples each were collected from each type of woodland area being investigated. The four samples in each lot were collected in a straight line at four-metre intervals, and whenever possible the second lot was taken from a line at right angles to the first. The soil samples thus collected were subjected to treatment within twenty-four hours of collection.

Each soil sample was emptied into a separate Petri dish and thoroughly mixed with a spatula: 1-2 g. of the soil were then transferred to a test-tube and weighed to the nearest 0.1 g. To this were added 2 c.c. of saturated aqueous picric acid solution, the whole being vigorously shaken, and thirty seconds later sufficient water to bring the total weight to ten times that of the original soil sample was added. The diluted sample was then vigorously shaken for one minute. One c.c. of this suspension was transferred to another test-tube; 9 c.c. of water were added and the whole was vigorously shaken for one minute. One c.c. of this soil suspension was transferred to another test-tube, and similarly diluted. One c.c. of the final suspension (original weight of soil diluted $\times 1000$) was transferred to each of six Petri dishes containing 10 c.c. of selective medium and to one dish containing plain malt agar. The control also served as a check on the identity of other organisms present in the sample. In addition to the above seven Petri dishes, another containing plain malt agar was inoculated with about 1 g. of untreated soil from the same sample, as a check on the presence of *Trichoderma* in very small quantity. The remainder of the sample was used for pH estimation. In a culture such as this, if *Trichoderma* is present in the soil, it will always be revealed by microscopical examination after about seven days incubation.

The eight dishes prepared thus from each sample were incubated at 23° C. and after seven days the colonies of *Trichoderma* were counted; a final count was made four days later to ensure that no slower-growing colonies of *Trichoderma* had been overlooked.

Colonies on this picric acid medium appear as hyaline, closely appressed mycelium with a few or no aerial hyphae in the centre; at a distance of about 0.5 cm. from the centre there is a zone of sparse aerial hyphae on which may be borne the characteristic conidiophores. This medium appears to cut down the sporing capacity of some strains to a considerable extent, and in many colonies no conidia are formed at all. Other strains, however, spore as profusely as on normal malt agar. In spite of this, *Trichoderma* colonies can readily be recognised with the naked eye after a little experience. The selective technique outlined above cannot be used to give an

accurate quantitative estimate of the *Trichoderma* in the soil, as a small percentage of the fungus may be killed, but as each sample was treated in the same way the number of colonies arising from each sample can be compared.

Woodland Areas Investigated.

In choosing the areas from which samples were to be taken, an attempt was made to find those within which the greatest number of woodland types existed on the same soil.

A. The Callender Estate in Falkirk.

This is situated at an average height of 150 feet above sea-level on a slope with a northern aspect. The underlying rocks in this area are coal measures. The superficial layers consist of humus varying in depth from 9 to 12 cm., below this a thin sand and gravel layer enters the northern part of the area but soon thins out and disappears. Under this and stretching down to the underlying coal measures is a layer of boulder clay between 3.25 and 6 metres deep. The soil samples were taken at the junction of the humus and boulder clay layers. The sand and gravel layer was only present in Series VI.

The area has borne trees for a very long period. Oak is the predominating tree, forming about two-thirds of the population, the remaining third being elm and beech with a few Scots pine. Certain areas have been cleared and re-afforested. Drainage throughout the whole area was good.

Soil samples were taken from the following areas between September 1949 and February 1950:

Series I. Mixed hardwood forest of great age, with *Rhododendron* and *Pteris* below. pH of soil 4.6-4.8.

Series II. Mixed hardwoods which had been clear felled one year previously. Herb layer of *Epilobium angustifolium* Linn., *Rubus* and *Pteris*. pH of soil 5.7-5.9. The herb layer had been cut back and cleared about two months before the samples were taken.

Series III. An area clear felled from mixed hardwoods in 1943 and replanted with Scots pine and larch in the ratio 3:1 in 1946. Shrub layer of *Rubus* and *Rhododendron*. pH of soil rather variable, 5.2-5.8.

Series IV. An area clear felled from mixed hardwoods in 1940 and replanted as in Series III in 1943. Shrub layer similar to Series III. pH of soil 5.8-6.0.

Series V. A plantation of *Picea sitchensis* Carr. approximately thirty years old; trees originally planted 1.5 metres apart but some

thinning had been carried out. Herb layer of *Asplenium filix-foemina* Bernh. mainly near the edges of the plantation. pH of soil 5.2-5.3.

Series VI. Parkland below hardwoods, and grazed by one or two horses. The tree layer was mainly oak, at 45-metre intervals, but samples were not collected under trees. Herb layer of mixed grasses. pH of soil 6.3-6.5.

Series VII. Taken for purposes of comparison from agricultural land 100 metres outside the wooded area. The field had just borne a crop of turnips and the land was fallow, with a number of annual weeds. pH of soil 6.4-6.6.

B. *The Hermitage of Braid in Edinburgh.*

This valley running east and west has steep sides and is heavily wooded. It is situated about 250 feet above sea-level. A thin layer of humus varying from 0 to 1 metre in thickness covers crumbling trachytic lavas of Old Red Sandstone age.

Although this valley has been wooded for a considerable number of years the woods are not so old as those on the Callender Estate. The predominating tree at the eastern end of the valley is beech; the western end, however, is rather more mixed. Soil samples were taken in January and February 1950.

Series VIII. Taken from the eastern end of the valley on the north-facing slope. Tree layer as above; underlying vegetation with scattered clumps of *Sambucus* and a few ferns. pH of soil 4.4-4.7.

Series IX. The western end of the valley on the north-facing slope. Tree layer 40 per cent. beech, the remainder being elm, ash and a few Scots pine. The underlying vegetation was similar to Series VIII with in addition some *Ranunculus ficaria* Linn. and *Chrysosplenium oppositifolium* Linn. pH of soil 4.5-5.0.

Series X. Taken for comparison from rough pastureland 90 metres outside the wooded area, grazed by sheep and cattle. Herb layer of mixed grasses with a little *Ulex europaeus* L. pH of soil 6.2-6.4.

Results.

It soon became evident that the number of *Trichoderma* colonies appearing in each dish of the selective medium was comparatively small; the total number of colonies appearing in the six Petri dishes was therefore recorded as representing the quantity of *Trichoderma* present in each respective sample. This total number of colonies in six dishes is hereafter called S6. The resulting S6 counts for all the samples collected are given below in Table I. The positive

or negative sign against each S6 number signifies whether or not the control dish, inoculated with untreated soil, showed the presence of a small quantity of *Trichoderma*.

It can be seen from Table I that of the 56 samples collected in woodland or recently clear-felled woodland soils 42 contained *Trichoderma*.

The pH values of the soils concerned (4.6-6.5) appeared to have little effect on the quantity of *Trichoderma* present. The number of colonies counted in each sample is consistently low; the highest (20 in Series IV) represents just over three colonies per dish for that sample.

A statistical examination of these results, using "Student's" method for the analysis of small samples as described by Paterson (1939), shows that only Series IV and VI may be considered to differ significantly from the remainder and that Series VI is significantly higher than Series IV.

Other Fungi Encountered in the Samples.

It was very noticeable that even after the selective treatment of the soil, colonies of *Penicillium* spp. outnumbered those of *Trichoderma* in almost all dishes. In one sample a species of the *Penicillium glabrum* group was encountered in such quantity that each

TABLE I.

Area History.		Hardwoods Undisturbed.			Hardwoods Recently Disturbed.			Land Outside Woods.			
Series No.	pH of Soil	I 4.7	VIII 4.6	IX 4.8	II 5.8	III 5.5	IV 5.9	V 5.1	VI 6.4	VII 6.5	X 6.3
S6 in each Sample.	Lot I	3+	0+	5+	0-	0-	4+	0+	7+	0-	1+
		0-	1+	0+	0+	0+	0-	1+	11+	3+	0+
		0-	0-	1+	0-	1-	0+	2+	2+	3+	0-
		3+	4+	0+	0-	0-	1+	0-	13+	2+	0-
S6 in each Sample.	Lot II	0+	0+	2+	3+	0+	20+	0+	16+	6+	0+
		4+	1+	0-	0+	0-	7+	1+	4+	0+	3+
		2+	1-	1+	2-	2+	1+	0-	1+	0+	0+
		4+	0+	4+	0+	2+	2+	3+	7+	2+	0-
TOTALS		16	7	13	5	5	35	7	61	16	4

of the six Petri dishes prepared from the sample yielded between 180 and 250 colonies. This represents a minimum of 180,000 units per gram of soil for that sample. It seems probable that this concentration was due to the presence in the soil of a profusely sporing pocket of the fungus. It was also noticed that *Cephalosporium curtipes* Sacc. and *Stachybotrys atra* Corda. were also almost always present in the dishes inoculated with untreated soil from woodland areas, although they were incapable of growth after the selective treatment of the soil.

DISCUSSION.

It is inevitable that the results obtained from a limited series of experiments such as this will not furnish sufficient evidence on which to build any theories as to the distribution of *Trichoderma* in woodlands. Many such experiments will have to be made covering a great number of different types of woods, occurring on many different soils, before anything like a complete picture can be obtained. Nevertheless, from the available evidence it is possible to say that *Trichoderma* appears to be a typical member of the microflora of acid soils under hardwoods and that if these hardwoods are cleared and later planted with conifers the fungus continues to exist in the soil. In the two areas investigated *Trichoderma* does not appear to be significantly more or less abundant in the soil just outside the influence of the trees. The fact that the number of colonies yielded by all samples is small suggests that at a depth of 10 cm. the fungus does not produce conidia profusely. The three series which gave the smallest counts of *Trichoderma* were taken from areas in which the soil had suffered recent disturbance, but as these values are not statistically significant, disturbance of the soil cannot be said to influence the fungus without much more supporting evidence. As regards the two series (IV and VI) which do differ significantly from the remainder, the exact reason for this is not easy to ascertain. There appear to be no factors common to both areas which are not also shared by others. In surface vegetation and recent history they differ markedly and they were not adjacent to one another.

As *Trichoderma* appears to be a common inhabitant of woodland soils, it must be considered as a possible controlling factor in the spread of those fungi, pathogenic to trees, which can also exist as saprophytes in the soil and which *Trichoderma* is capable of parasitizing. Investigation of the ecology of this fungus would therefore be desirable and it is hoped to continue this work in the future.

SUMMARY.

1. Ten isolates of *Trichoderma*, the majority of which were taken from the soil, were opposed to two strains of *Armillaria mellea* and one of *Polyporus schweinitzii* on parallel, hanging malt agar smears at pH 3.4-5.1 and 7.0.

All ten isolates of *Trichoderma* were identical in their action towards *Armillaria*. At pH 3.4, when the two mycelia met on the medium, *Trichoderma* hyphae coiled around those of the host. Penetration was occasionally observed, but more often the hyphae of *Trichoderma* grew in close contact with those of the host, which later showed signs of deterioration. The formation of groups of crystals in the medium was not observed. Subsequent failure to subculture the *Armillaria* colony indicates that it had been killed. When the two mycelia met on the glass between the agar smears, parasitism took place only at the points of actual hyphal contact.

On a medium of pH 5.1 parasitism was clearly evident, though apparently it was less severe than on the more acid medium. On a medium of pH 7.0 no signs of parasitism could be observed.

The rhizomorphs of *Armillaria* when invested by *Trichoderma* hyphae stopped growing after a few days. Later, however, the hyphal tips were transferred to fresh medium and continued to grow, indicating that the *Trichoderma* had no permanent toxic effect.

2. *Polyporus schweinitzii* was parasitised by *Trichoderma* on a medium of pH 3.4. Hyphae of *Trichoderma* in contact with *P. schweinitzii* on the agar medium cause deterioration of the host hyphae. On one occasion only, crystals were seen to form in the medium in the area of parasitism. Chlamydospores of *P. schweinitzii* formed on the glass between the smears were readily invested by the hyphae of *Trichoderma*, but no evidence of deterioration could be observed. On media of pH 5.1 and 7.0 no evidence of parasitism could be observed.

3. For the investigation of the quantitative ecology of *Trichoderma* in woodland soils selective medium was developed, based on the tolerance of the fungus to picric acid. *Trichoderma* appears to be a typical member of an acid woodland soil flora. The quantity present in these woodland soils does not appear to differ markedly from that found in similar soils outside the influence of the trees and in both these areas *Penicillium* is more prevalent than *Trichoderma*.

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EXPLANATION OF PLATE VI.

1. Hyphae of *Trichoderma* growing in close proximity to the broader hyphae of *Armillaria mellea*, which in places show signs of vacuolation. A tendency to branch profusely is seen in the *Trichoderma* hyphae, together with a weak tendency to coil round the host. (× 250.)
2. Hyphae of *Trichoderma* growing closely alongside the broader hyphae of *Armillaria mellea*. Near the centre a small branch hypha has penetrated the host. (× 250.)
3. A thin branch hypha of *Trichoderma* has penetrated the broader hypha of *Armillaria mellea*, and, after emerging, has continued to grow alongside, forming three penetration initials. (× 250.)
4. The thinner, more distinct *Trichoderma* hyphae towards the top of the photograph are closely adjacent to the *Armillaria* hyphae which were growing in the general direction of the bottom of the photograph. In the latter position, where the two types of hyphae have been in contact for a longer period, marked disintegration of the *Armillaria* can be seen. This is less obvious towards the top, where contact has been shorter. (× 75.)
5. In the centre, a chlamydospore of *P. schweinitzii* is closely invested by *Trichoderma* hyphae. Almost all the hyphae of the former are empty, following chlamydospore formation. (× 500.)
6. A chain of chlamydospores of *P. schweinitzii*, with empty hyphae between them, invested by hyphae of *Trichoderma*. Loose conidia of the latter can be seen in a drop of moisture in the upper half of the photograph. (× 250.)



1



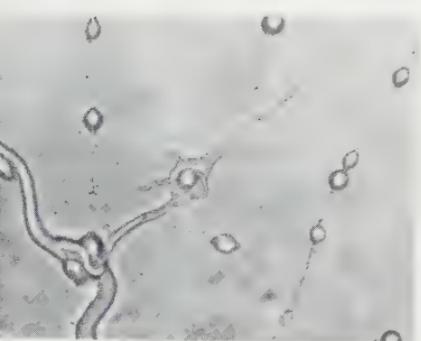
2



3



4



5



6

1-4. *Trichoderma* with *Armillaria mellea*.

5 and 6. *Trichoderma* with *Polyporus schweinitzii*.

(For explanation see p. 114.)

SOME DESMIDS FROM WEST HIGHLAND LOCHS.

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(Read by title, 20th November 1952.)

Our knowledge of the plankton of Scottish lochs is based largely on the investigations of Roy and Bissett (1893), and on the collections made by W. and G. S. West (1903, 1905, 1912). During the last few years, numerous collections have been made during the summer from lochs in various parts of the West Highlands. The main collecting grounds were the Moor of Rannoch, South Uist, and around Loch Torridon, but there were also some very productive lochans in the hills north of Loch Duich. Detailed accounts of these collections will be published, but meanwhile it seems desirable to place on record a number of desmids which have never, or only rarely, been reported for Scotland.

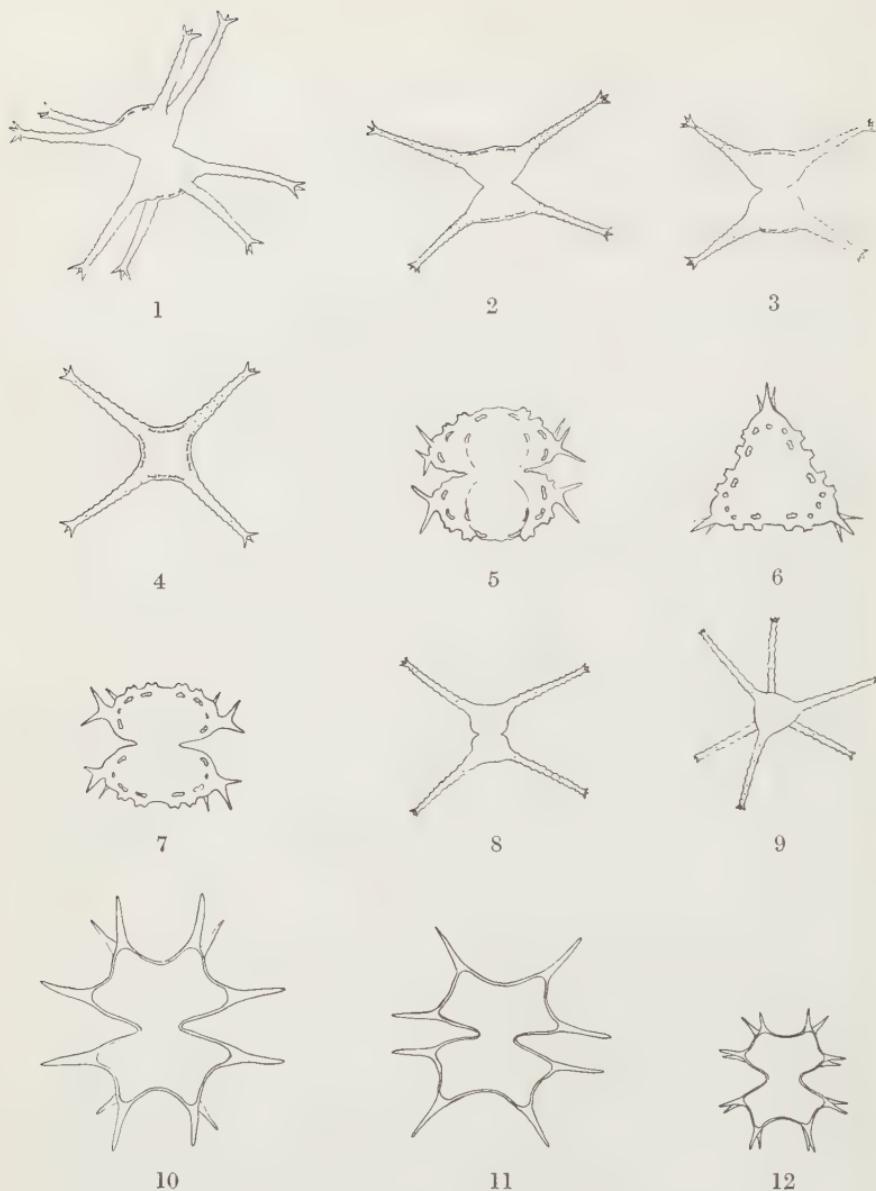
In the following descriptions, Pl. 1, Pl. 2 and Pl. 3 refer to a series of shallow lochs surrounded by bog at 1500 feet above sea-level, about four miles due east of Dornie. Pl. 1 is named Loch nan Eun; Pl. 2 and Pl. 3 are small lochans near Loch nan Eun, Pl. 3 being the more peaty. T.16, T.17 and T.18 refer to a group of small lochans surrounded by bog on the high ground behind Diabeg in Wester Ross.

DESCRIPTIONS OF SPECIES.

STAURASTRUM ANATINUM var. *LONGIBRACHIATUM*, W. & G. S. West
(text-fig. 1; 1, 2, 3, 4).

This desmid was plentiful in Loch Ossian, but always in a quadri-radiate form. Most specimens had shorter processes and more cup-shaped semi-cells than the type, but a few quite typical individuals were seen. The single row of verrucae were just within the margin and rarely showed in vertical view unless the specimen was slightly tilted. In a previous paper (Lind, 1950) this desmid is referred to as a form of *S. anatinum*. Further investigation, and the discovery of forms with longer processes and more trapeziform cells, leads to its inclusion in *S. anatinum* var. *longibrachiatum*.

Length without processes $39-44\mu$; with processes $79-92\mu$. Breadth without processes $27-31\mu$; with processes $92-133\mu$. Isthmus $14-15\mu$.



TEXT-FIG. 1.—DESMIDS FROM WEST HIGHLAND LOCHS.

1-4: *STAURASTRUM ANATINUM* var. *LONGIBRACHIATUM* W. & G. S. West. ($\times 205.$)5-7: *STAURASTRUM CORNUTUM* Archer. ($\times 410.$)8, 9: *STAURASTRUM PARADOXUM* var. *EVOLUTUM* W. & G. S. West. ($\times 410.$)10, 11: *ARTHRODESMUS OCTOCORNIS* Ehrenb. forma *IMPAR* Jacobs. ($\times 410.$)12: *XANTHIDIUM SMITHII*. ($\times 410.$)

STAURASTRUM CERASTES Lund.

This desmid, previously recorded for localities in Aberdeenshire, Raasey and Sutherland, occurred in three small lochs on the Moor of Rannoch.

STAURASTRUM CORNUTUM Archer (text-fig. 1; 5, 6, 7).

This species was first found by Archer in Connemara, and was exhibited, with a short description, at a meeting of the Dublin Microscopical Club (Archer, 1881). Archer deferred a full description, while giving it the name *cornutum* because it had stout horned spines. Roy (1893) describes the species more fully and records it for two Scottish localities. A desmid found in Pl. 3 and T.17 agreed with the description by Roy, except that it was slightly larger. Length, 32μ . Breadth without spines, 31μ ; with spines, $39\cdot6\mu$. Roy gives the size as 27μ long and 27μ wide without spines; spines 9μ . Grönblad (1921) has described a quadriradiate form; from its size and from the concave walls in vertical view, however, this would appear to be a form of *S. forficulatum* Lund var. *heteracanthum* Grönblad.

STAURASTRUM DICKIEI var. **CIRCULARE** Turn.

This desmid occurred in a reservoir near Elgol in Skye. It does not seem to have been recorded previously for Scotland.

STAURASTRUM GLADIOSUM Turn.

This was found in Pl. 1, Pl. 2, and T.18, and has not previously been recorded for Scotland.

STAURASTRUM NATATOR West.

This species occurred in Pl. 1. It has previously been recorded only for Rhiconich, Sutherland.

STAURASTRUM PARADOXUM var. **EVOLUTUM** W. & G. S. West (text-fig. 1; 8, 9).

This species, previously recorded for Shetland, was seen in T.16, T.17 and T.18.

STAURASTRUM OPHIURA var. **CAMBRICUM** W. & G. S. West.

This variety, previously recorded only from Wales, occurred in Pl. 1. The shorter, strongly-converging processes and very distinct

conical nodules serve to distinguish it from the type. The Scottish specimen, which had eight rays, was 68μ long and 100μ broad, including processes.

ARTHRODESMUS BULHEIMII Raub.

This species, which has previously been recorded for Harris and Sutherland, was found in Pl. 3.

ARTHRODESMUS OCTOCORNIS Ehrenb. forma IMPAR (Jacobs) (text-fig. 1; 10, 11).

This desmid was recorded by Roy and Bissett (*loc. cit.*) from one locality, and West (1912) expresses some doubt about including it in *A. octocornis*, suggesting that it would be better placed in *Xanthidium Smithii*. A specimen which occurred in Pl. 3 is undoubtedly this same desmid. Length without spines $42\text{--}49\mu$; with spines $76\text{--}80\mu$. Breadth without spines $34\text{--}42\mu$; with spines $76\text{--}80\mu$. Isthmus $10\text{--}13\mu$. Maximum length of spine 23μ .

Grönblad (1921) describes the same desmid which he renames *Arthrodесmus impar* (Jacobs). *Xanthidium Smithii* occurred in the same collection (Pl. 3) and a figure is given for comparison (text-fig. 1; 12). It was always smaller than *A. octocornis* forma *impar*, and had regularly two spines at each corner.

ARTHRODESMUS INCUS var. VALIDUS.

This very distinct variety of *A. Incus*, which has previously been recorded only for Sutherland, was also found in Pl. 3.

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THE VEGETATION OF THE ISLAND OF SOAY, INNER HEBRIDES.

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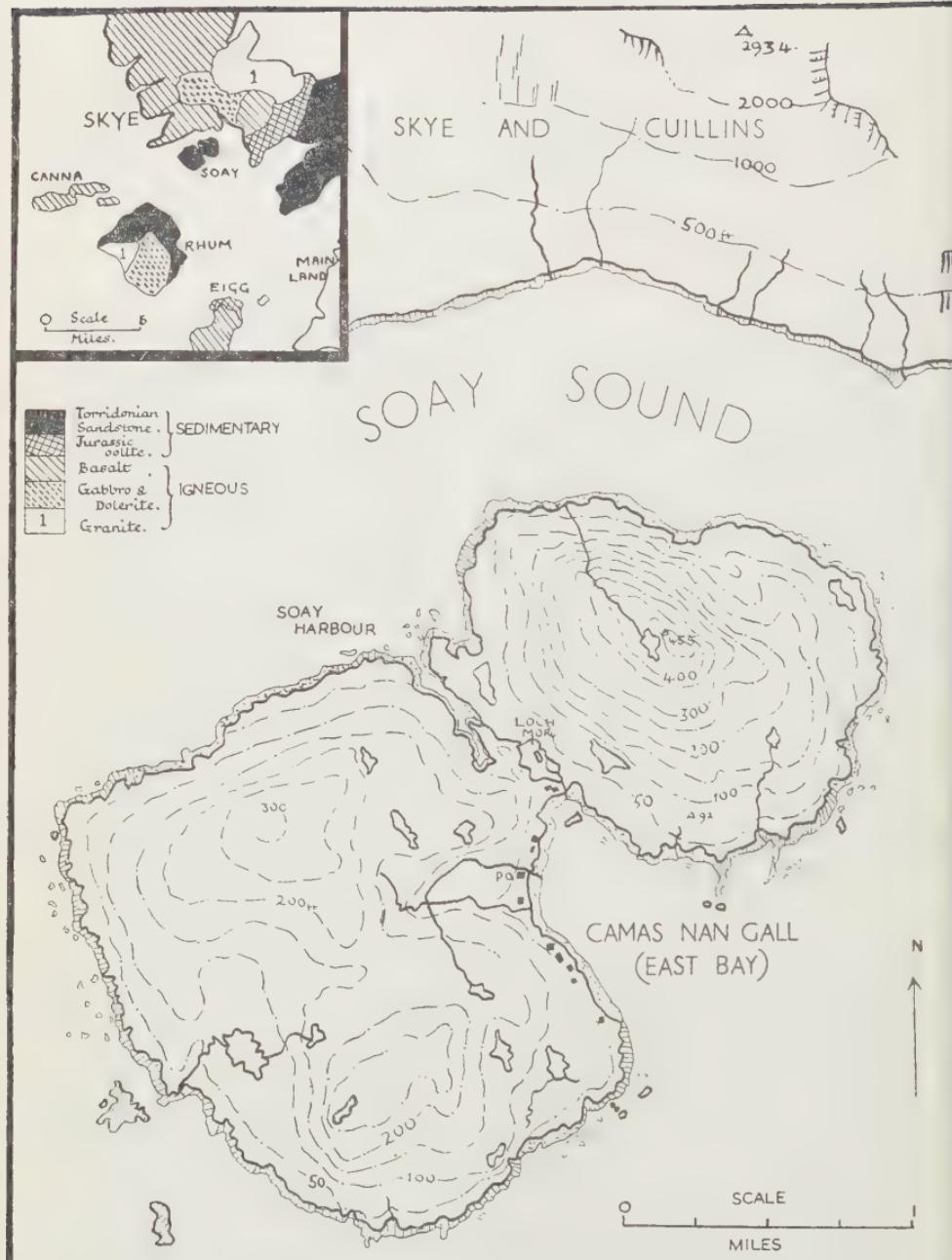
INTRODUCTION.

The following short account is the result of a survey made during two visits of a total length of three weeks, to the island of Soay, at the end of July 1948 and 1949. The field work was carried out in conjunction with M. M. Parker and the late Miss A. M. Broadbent. Although in recent years several floristic surveys have been made within the Hebrides (e.g. Campbell, 1936, 1937, 1941, 1945; Harrison, 1937, 1939), little ecological work appears to have been carried out on Hebridean vegetation, apart from that of Petch (1933) and Poore and Robertson (1948) on St. Kilda, and of Asprey (1947) on Canna and Sanday. The following account is therefore presented as a small contribution to a further knowledge of the region.

Soay is situated in the Inner Hebrides (text-fig. 1) and is almost completely surrounded by land. The island, which is divided into two halves connected only by a narrow isthmus, is about three miles long, with a maximum width of two miles. The basic rock is almost entirely Torridonian Sandstone. The narrow neck of land between the Bay and the Harbour reaches a height of 50 feet only in localised areas, and the presence of gravel below the peat in this isthmus indicates that the region was once a strait between the two halves of the island (Harker and Clough, 1904). This is corroborated by a peat boring (Blackburn, 1940) in Loch Mor, which shows marine diatoms several feet down. The surface of the island is undulating, with a maximum height of 450 feet. Cliffs occur all round the coast; the highest reach 50 feet on the Atlantic side, but boulders and large pebbles form local beaches, including that of Camas nan Gall. There are several lochs of varying character, but few fast-flowing burns, which in summer may dry up completely.

According to local report, the island has been inhabited for at least two hundred and fifty years, and the population, although reaching one hundred and fifty within living memory, is now only forty. All the houses are aggregated round Camas nan Gall,

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TEXT-FIG. 1.—Isle of Soay and Cuillins of Skye.

except for a small and now disused shark factory by the harbour. The effect of the population on the vegetation has therefore been largely confined to the eastern coast, apart from the grazing of a very limited number of cows and sheep, the remaining vegetation being unmodified except for the irregular firing of *Calluna* in the coastal regions. With the exception of small gardens, cultivation occurs only in the isthmus, where potatoes are grown. Hay is also cut here and peat excavated from a few small sites. Except for a few localised efforts in relation to a now-abandoned scheme to import grouse, no other attempt has been made to drain the peat. The vegetation of these cultivated regions is not recorded since it has no bearing on the general interpretation of the vegetation.

VEGETATION.*

1. *Woodland.*

Although there is very little natural woodland at the present time, its occurrence is an unusual feature since it is well developed in comparison to that of neighbouring islands. It is found only on steep, well-drained slopes or scree, or in deep gullies sheltered from the wind, the soil in all areas being fairly dry. No areas of woodland are extensive, but all those studied had a similar composition. The trees, which were usually branched only near the tops, have an average height of 5–7 m. and a distance apart of 1–2 m., forming an almost closed canopy.

According to the results of a peat boring by Blackburn (1940) the island supported in Boreal times birch, pine and a large amount of hazel, and in Atlantic times alder, oak and elm. The dominant trees at present are species of *Salix*, *Betula* and *Sorbus aucuparia*, there being an almost entire absence of these species, other than in scrub form, on neighbouring islands. Only three trees of *Corylus avellana* were found, and two specimens of *Quercus petraea*, occurring within a few metres of each other. This is noteworthy, since the species was not found elsewhere on the island and is reported in other regions of the Hebrides only from Rhum and Eigg (Harrison, 1939). It is possible that they may have grown from acorns accidentally introduced by visitors or in cargo, since both were near the harbour.

The herb layer, as seen in Table 1, is rich in species. Though a few bog and moor species such as *Calluna*, *Vaccinium myrtillus* and *Molinia caerulea* do occur, they have a low frequency, and the majority of species are confined to woodland. The moss layer is

* All species of vascular plants are named in accordance with the *Flora of the British Isles* (Clapham, Tutin and Warburg, 1952).

TABLE 1.—WOODLAND SPECIES.

TREE LAYER.						
<i>SALIX CAPREA</i>					<i>BETULA VERRUCOSA</i>	
<i>S. AURITA</i>					<i>B. PUBESCENTS</i>	
<i>S. ATROCINEREA</i>					<i>CORYLUS AVELLANA</i>	
<i>SORBUS AUCUPARIA</i>					<i>QUERCUS PETRAEA</i>	
SHRUB LAYER.						
<i>LONICERA PERICLYMENUM</i>		<i>f</i>			<i>ROSA CANINA</i> agg. . . .	
<i>RUBUS</i> sp. . . .		<i>o</i>				
HERB LAYER.						
<i>OXALIS ACETOSELLA</i>		<i>f</i>			<i>GALIUM HERCYNICUM</i>	
<i>VIOLA RIVINIANA</i>		<i>f</i>			<i>STACHYS SYLVATICA</i>	
<i>VACCINUM MYRTILLUS</i>		<i>f</i>			<i>SEDUM ANGLICUM</i>	
<i>TEUCRIUM SCORODONIA</i>		<i>f</i>			<i>HYPERICUM PERFORATUM</i>	
<i>PRUNELLA VULGARIS</i>		<i>f</i>			<i>DIGITALIS PURPUREA</i>	
<i>LYSIMACHIA NUMMULARIA</i>		<i>f</i>			<i>ANEMONE NEMOROSA</i>	
<i>MOLINIA CAERULEA</i>		<i>f</i>			<i>SCROPHULARIA NODOSA</i>	
<i>HOLCUS LANATUS</i>		<i>f</i>			<i>FESTUCA OVINA</i>	
<i>DE SCHAMPSIA FLEXUOSA</i>		<i>f</i>			<i>BRACHYPODIUM SYLVATICUM</i>	
<i>AGROSTIS TENUIS</i>		<i>f</i>			<i>JUNCUS ACUTIFLORUS</i>	
<i>JUNCUS EFFUSUS</i>		<i>f</i>			<i>CAREX BINERVIS</i>	
<i>FRAGARIA VESCA</i>		<i>o-f</i>			<i>C. NIGRA</i>	
<i>JUNCUS CONGLOMERATUS</i>		<i>o-f</i>			<i>HYPERICUM ANDROSAEUM</i>	
<i>J. ARTICULATUS</i>		<i>o-f</i>			<i>ENDYMION NON-SCRIPTUS</i>	
<i>AJUGA REPTANS</i>		<i>o-f</i>			<i>DRYOPTERIS FILIX-MAS</i>	
<i>POTENTILLA ERECTA</i>		<i>o-f</i>			<i>PTERIDIUM AQUILINUM</i>	
<i>PRIMULA VULGARIS</i>		<i>o</i>			<i>POLYPODIUM VULGARE</i>	
<i>CIRCAEA LUTETIANA</i>		<i>o</i>			<i>BLECHNUM SPICANT</i>	
<i>CALLUNA VULGARIS</i>		<i>o</i>			<i>ASPLENIUM RUTA-MURARIA</i>	
<i>ERICA CINEREA</i>		<i>o</i>			<i>HYMENOPHYLLUM WILSONI</i>	
<i>SOLIDAGO VIRGAUREA</i>		<i>o</i>				
MOSS LAYER.						
<i>THUIDIUM TAMARISCINUM</i>					<i>CAMPYLOPHUS SHAWII</i>	
<i>HYPNUM CUPRESSIFORME</i>					<i>PLAGIOCHILA ASPLENOIDES</i>	
<i>EURHYNCHIUM PRAELOONGUM</i>					<i>PLEUROZIA PURPUREA</i>	
<i>HYPNUM SCHREBERI</i>					<i>SACCOGYNIA VITICULOSA</i>	
<i>MNIUM UNDULATUM</i>					<i>ODONTOSCHISMA SPAGNI</i>	
<i>M. HORNUM</i>					<i>PELLIA EPIPHYLLA</i>	
<i>HYLOCOMIUM SQUARROSUM</i>					<i>LEPTOSCYPHUS TAYLORI</i>	
<i>POLYTRICHUM FORMOSUM</i>					<i>CEPHALOZIA MACROSTACHYIA</i>	
<i>RHACOMITRIUM LANUGINOSUM</i>						
<i>PLAGIOTHECIUM UNDULATUM</i>					<i>LOBARIA LAETEVIRENS</i>	
<i>ULOTA CRISPA</i>					<i>CLADONIA SYLVATICA</i>	
<i>HYPNUM CRISTA-CASTRENSIS</i>					<i>C. UNCIALIS</i>	
					<i>C. PYXIDATA</i>	
					<i>C. RANGIFERINA</i>	

also remarkably abundant and rich in species, often reaching a height of 2-3 cm. *Thuidium tamariscinum*, *Hypnum schreberi* and *H. cupressiforme* were co-dominant, and between them the herb

and the moss layer completely clothed the ground, rocks, dead branches, etc. In many parts even the branches and trunks of living trees were green with *Hypnum* spp.; tufts of *Ulota crispa* occurred up to a height of 4 m. and *Oxalis acetosella* rooted up to 1½ m. Numerous fallen branches and trunks littered the ground, and many of the standing trees were leaning at unusual angles or were dead.

In no cases were seedlings or young saplings found in woodland itself, and apart from saplings of *Betula* and *Salix*, which occurred in valleys, on small ledges, or along river-banks, thus demonstrating the fertility of the adult trees, evidence of regeneration was rare. One area was found, however, with an abundance of seedlings, close to a small wooded slope. The vegetation outside the wood consisted of *Empetrum* and *Calluna*, the former an unusual dominant; and *Vaccinium myrtillus*, *Molinia*, and *Trichophorum caespitosum* were common in a matrix of dense *Hypnum schreberi*. The tree species were as follows:

	WITHIN WOOD.	NUMBER OF TREES PER 25 SQ. METRES.	
		25 m. away.	60 m. away.
<i>Mature</i>			
BETULA	.	co-d	..
SORBUS	.	co-d	..
SALIX	.	f	..
<i>Seedlings</i>			
BETULA	.	..	35
SORBUS	.	..	6
SALIX

This area of regeneration may possibly be accounted for by the occurrence together of the following: proximity of seed parents to sufficiently dry and sheltered ground, absence of *Sphagnum* (which is known to check certain conifer seedlings), a warm sheltering weft of *Hypnum schreberi* and sufficient light.

It would seem, then, that the wood is beyond its climatic limits. The steep slopes, cliffs and gullies (mainly north-facing), to which woodland is limited, and which are the only regions providing good drainage and shelter from winds, have the disadvantage of a low light intensity and an almost entire absence of direct sun rays. The

moribund appearance and declining angles of many of the trees suggest further that the soil in such positions may be insufficiently deep for the maintainance of trees beyond a certain size. The fact that woodland occurs at all on Soay, in comparison to neighbouring treeless islands, is probably due to the proximity of the sheltering 3000 feet Cuillins.

2. *Callunetum*.

This community occurs almost exclusively on hilltops, particularly round the coast. The peat is usually shallow, often as little as 6 cm. deep, and occasionally bare rock-faces are exposed. It is the driest peat on the island and is very dark in colour. The species recorded in Table 2, V, show that the total is large, but only a few, such as *Calluna*, *Potentilla erecta*, *Deschampsia flexuosa*, and *Hypnum cupressiforme* were always present. *Pteridium aquilinum* occurs occasionally, though in stunted form, in all except the most exposed areas, but it typically increases abruptly to dominance on hillsides and valleys in localised regions, where it may reach a height of $\frac{1}{2}$ –1 m. and cause complete suppression of *Calluna*, which can grow very vigorously in such a position when *Pteridium* is absent. *Vaccinium myrtillus* increases in frequency on small knolls, but is always stunted. The moss layer, whose dominant species together with *Cladonia* spp. occurred in a loose weft throughout the *Callunetum*, increased in luxuriance where the *Calluna* was "leggy" and unfired. *Trichophorum cespitosum* and *Molinia* became more frequent in *Callunetum* adjacent to areas in which these two species were dominants. *Empetrum nigrum* became dominant in one small area in which peat hagsgs reached a height of 1 metre.

Stages in regeneration after burning were incidentally observed. After recent firing, the bare peat was very slippery, owing to a slimy layer of *Gleocapsa* and *Aphanocapsa* spp., with fungal hyphae and, rarely, liverworts and *Cladonia* spp. in the small cracks. Later, seedlings of the 4–8 leaf stage of *Calluna* and *Erica cinerea* become very obvious, 61 such seedlings being counted in a square foot. There appears to be no evidence that *Trichophoretum* tends to replace *Callunetum*, with firing, on Soay as suggested by Fraser (1933) for Western Scotland. The following cryptogams were collected from *Callunetum*: *Hypnum cupressiforme*, *H. schreberi*, *Rhacomitrium lanuginosum*, *Dicranum majus*, *Thuidium tamariscinum*, *Cephalozia connivens*, *C. macrostachya*, *C. bicuspidata*, *Lepidozia setacea*, *Calypogeia trichomanes*, *Lophozia alpestris*, *Leptoscyphus taylori*, *Cladonia pityrea*, *C. uncinalis*, *C. sylvatica*.

3. *Festuca-Agrostis* Grassland.

This community occurred extensively only on one slope, and the species present were very similar to those recorded by Asprey (1947)

TABLE 2.—BOG AND MOOR SPECIES.

	I.	II.	III.	IV.	V.
	SPHAGNETA.		TRICHO- PHORETUM.	MOLINIETUM.	CALLUNETUM.
SPHAGNUM CUSPIDATUM.	d
SP. PLUMULOSUM	d	o
LENYANTHES TRIFOLIATA	a
POTAMOGETON NATANS	a	o-f
RHYNCOSSPORA ALBA	f	ld	o
TRIOPHORUM ANGSTIFOLIUM	f	f
SPHAGNUM CYMBIFOLIUM	r	d	a
SP. PAPILLOSUM	r	a	vr	r	..
DROSERA ROTUNDIFOLIA	o	a	o-a	c	o-r
ERICA TETRALIX	o	a	lf	d	f
TRICHOPHORUM CAESPITOSUM	vr	lf	d	o-a	
LYRICA GALE	r	lf	o	r	o-r
CALLUNA VULGARIS	..	a	a-co-d	a-co-d	d
COLONIA CAERLEA	..	lf	a	d	la
SPHAGNUM ACUTIFOLIUM	..	a	o.r.	la	lf
TENELLUM	o	o.f.	c
MEDIUM	o.f.	vr	vr
AREX BINERVIS	r	o.f.	
POLYGALA SERPYLLIFOLIA	vr	vr	
POTENTILLA ERECTA	o	o.f.	f
CUPHRASIA sp.	..	f	o	..	o
LADONIA SYLVATICA	..	f	f	..	f
TRIOPHORUM VAGINATUM	..	vr	o-f	o	r-f
INGUICULA VULGARIS	..	r	o	o	r
ERICA CINEREA	r	o	a
AREX ECHINATA	..	f	o
NIGRA	..	f	o
UNCUS SQUARROSUS	..	f	o
DROSERA ANGLICA	..	o	r
INGUICULA LUSITANICA	..	vr
ESCHAMPSIA FLEXUOSA	f	f
MIMPETRUM NIGRUM	la
ACCINUM MYRTILLUS	f
TERIDIUM AQUILINUM	la

on Canna. The limited extent of this community on Soay is probably to be associated with the slight grazing on the island, restricted mainly to this one slope. The small area of the community, however, is not sufficient to influence communities dominated by *Calluna*, *Trichophorum* and *Molinia*, though the lists from these communities on Canna are obviously augmented by grassland species such as *Agrostis tenuis*, *A. canina*, *Anthoxanthum odoratum*,

Nardus stricta, *Succisa pratensis*, *Lotus corniculatus* and *Lathyrus pratensis*.

4. *Molinietum*.

Molinietum occurs on wetter peat than do the previously mentioned communities, and usually on sloping, well-drained areas. Where it is dominant, *Molinia* is always luxuriant, reaching a height of 25–40 cm., average tussocks being 12–15 cm. in diameter. Pure *Molinietum* is rare, since the erosion of peat on the slopes on which it occurs is accompanied by abundant *Calluna* and local tussocks of *Trichophorum caespitosum*. The species present are recorded in Table 2, IV.

5. *Trichophoretum*.

This community, consisting almost entirely of large low uniform tussocks, up to a height of 15 cm. and a diameter of 8–10 cm., is not common in a pure state except on very gradually sloping hillsides, but admixed or co-dominant with *Molinia* and *Calluna* it occurs extensively, particularly over large flat expanses, accompanied by species shown in Table 2, III. Species not present in *Molinietum*, or found with a greater frequency in *Trichophoretum*, are *Eriophorum angustifolium*, *Rhyncospora alba*, and several species of *Carex*. The absence of *Deschampsia flexuosa* is marked. Species of *Sphagnum* are found in wet hollows, but mosses are not abundant. The peat is firm and fairly dry, though often quaking, and erosion is not noticeable. There was little evidence that this community formed a climatic climax on Soay, as suggested by Fraser (1933) for Western Scotland, though such a community may be a late stage in the “basin succession” he suggests from open water through *Sphagnetum*.

6. *Sphagnetum*.

This community occupies extensive and usually remarkably flat areas several hundred metres wide. The substratum is water-logged and not firm enough to walk on in many places. In such areas it is usual to find a pool or loch of open water in the centre, the margins grading almost imperceptibly into a transition region where the substratum is unconsolidated. Species, including submerged *Sphagnum*, occur as recorded in Table 2, I. Concentric to this zone, *Sphagnetum*, as recorded in Table 2, II, is found. The *Sphagnum* species here form a hummocky matrix in which such species as *Erica tetralix* and *Calluna* reach a height of 20 cm., with abundant *Cladonia sylvatica* on the stems. *Trichophorum* and

Molinia, though locally common, are poor and diffuse in form, though on drier ground the community may grade into *Trichophoretum*, which forms yet another concentric zone.

7. Water Systems.

There are several fast-flowing burns with rocky beds and banks. No vascular species were found in the water itself, and the marginal

TABLE 3.—VALLEY COMMUNITIES.

	I.	II.	III.	IV.
SPHAGNUM ACUTIFOLIUM				
S. TENELLUM . . .	co-d	o
S. MEDIUM . . .				
POLYTRICHUM COMMUNE . . .	co-d
MENYANTHES TRIFOLIATA . . .	lf
EQUISETUM FLUVIATILE . . .	o
POTAMOGETON NATANS . . .	vr
JUNCUS SQUARROSUS . . .	vr	vr
CAREX BINERVIS . . .	r	o
C. ECHINATA . . .	r	o
MYRICA GALE . . .	vr	lf	d	..
TRICHOPHORUM CAESPITOSUM . . .		r-f	vr	..
FESTUCA OVINA . . .	ld-d	lf
POTENTILLA ERECTA . . .	f	o-f	r	o
HYDROCOTYLE VULGARIS . . .	a	f	r	o
JUNCUS EFFUSUS . . .	a	a	o	f
J. CONGLOMERATUS . . .	a	f	f	a
J. ARTICULATUS . . .	a	o	o	a
RANUNCULUS FLAMMULA . . .	a	a	o	e
MOLINIA CAERULEA . . .	r	d	f	lf
HOLCUS LANATUS . . .	lf	f	..	f
VIOLA PALUSTRIS . . .	f	f	..	f
ANTHOXANTHUM ODORATUM . . .	r	o	..	o
PEDICULARIS SYLVATICA . . .	o	o
AGROSTIS TENUIS	o	..	f
PEDICULARIS PALUSTRIS	r
MIMULUS GUTTATUS	r
IRIS PSEUDACORUS	o
LYCHNIS FLOS-CUCULI	lf
PHRAGMITES COMMUNIS	d

species varied with the communities through which the burns ran, in rocky regions *Salix* and *Pteridium* being common. *Calluna* and *Erica tetralix* were often found on large rocks above the water-level in the middle of the burns, surviving on almost negligible depths of soil. Lochs were of two types; some had rocky margins, with a rocky, gravel, or silted base, as far as visible. The water was slightly

alkaline, often supplied from a fast-flowing burn, the loch usually being drained by water flowing slowly through a valley containing one of the types of vegetation listed in Table 3. The species found in these lochs were *Nymphaea alba*, *Equisetum fluviatile*, *Lobelia dortmanna*, *Eleocharis palustris*, and *Sparganium minimum*. The second type of loch is smaller and corresponds to that mentioned under *Sphagnetum*, always surrounded by the latter community. The margins are barely visible, and as far as could be seen the bottoms are covered with *Sphagnum* spp. The water at the margins is acid and there is no apparent drainage. Species found in such lochs are *Phragmites communis*, *Equisetum fluviatile*, *Potamogeton natans*, *Menyanthes trifoliata*, and submerged species of *Sphagnum*.

In valleys and small catchment areas up to about thirty metres in width, water could be seen flowing along one side of the vegetation, or could be heard trickling underground; occasionally in coastal regions convincing proof of water-flow was given by the formation of waterfalls over the cliffs to the sea. The communities most commonly found were those dominated by *Sphagnum* spp. and *Festuca ovina* as in Table 3, I. Occasionally such habitats bore *Molinietum*, e.g. Table 3, II, and the latter association and *Myricetum* (Table 3, III) were typical of water-logged, almost swamp-like areas. In such positions *Molinia* and *Myrica* were more luxuriant than elsewhere on the island. When water flowed slowly over a gravel substrate, as observed in two places where a burn flowed into the sea, an association dominated by *Phragmites* was found (Table 3, IV).

8. Cliff Flora.

According to the islanders, the tops of all cliffs are reached in rough weather by sea spray, though the sides of some gullies are too high or far back to be affected. The following species typical of coastal areas were noted, though in comparison with *Canna* there is no sand-dune formation.

(a) Small ledges exposed to wind and spray.—A fine turf was found composed of *Plantago maritima*, *P. coronopus*, *P. lanceolata*, *Armeria maritima*, *Sedum anglicum* and *Festuca ovina*, with occasionally *Trifolium repens* and *Thymus serpyllum*.

(b) More sheltered positions, e.g. the walls of gullies running down to the sea.—No closed community was found here, but isolated species of *Cochlearia officinalis*, *Polypodium vulgare*, *Sedum anglicum*, *S. rosea*, and, where water trickled, *Hydrocotyle vulgaris*.

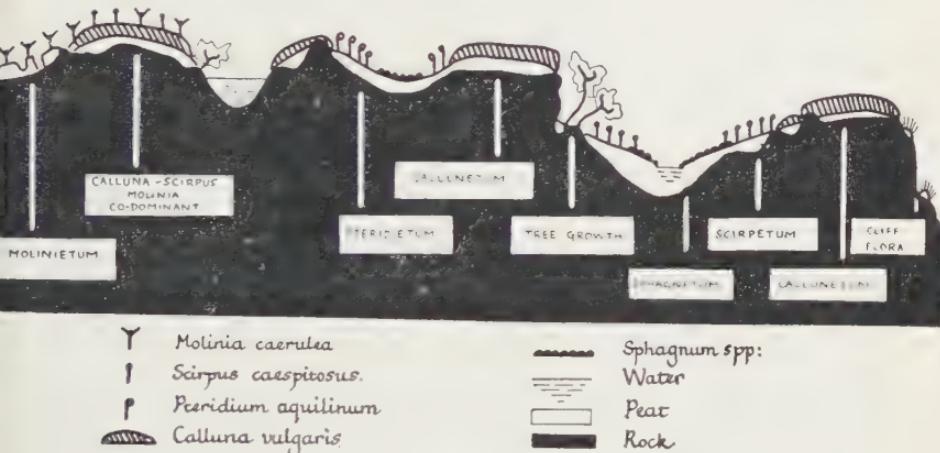
(c) Rocks and boulders of beaches and gully bottoms beyond the reach of the highest spring tides.—Again there was no closed

community of plants, and typical species were *Scutellaria minor*, *Potentilla anserina* and *Galium aparine*.

(d) Cliff tops.—Plants of this habitat replaced or modified Callunetum and were mainly *Festuca ovina*, *Empetrum nigrum*, *Salix repens*, *Holcus lanatus*, *Deschampsia flexuosa*.

A hypothetical reconstruction of part of the island given in text-fig. 2 shows the vegetation typical of the various habitats.

→ Prevailing wind



TEXT-FIG. 2.—Hypothetical reconstruction of part of the island to show the vegetation typical of various habitats.

The points to be noticed in this diagrammatic summary are:

1. Cliff flora, limited to ledges.
2. Cliff-top Callunetum, on shallow irregular peat, with hagging.
3. Callunetum grading into Trichophoretum on gentle slopes, associated with deeper peat.
4. Trichophoretum grading into Sphagnetum, and this latter into open water.
5. Tree growth on steep rocky scarps sheltered from wind.
6. Inland Callunetum not so markedly eroded as in coastal areas.
7. Pteridetum abruptly developed on sides of small valleys and hollows, the latter being dominated by *Sphagnum* or marsh species, at the base.
8. Loch with rocky margins and base, uncolonised by *Sphagnum*.
9. Callunetum sometimes intermingled with Trichophoretum and Molinietum, the latter on steeper well-drained slopes.

CONCLUSION.

From the above account it thus appears that the communities found on Soay accord on the whole with those previously defined by Tansley for areas of similar climatic and edaphic conditions, *i.e.* communities dominated by *Calluna*, *Molinia*, *Trichophorum*, and *Sphagnum* spp. Some communities listed by Tansley are, however, missing. *Vaccinietum myrtilli* does not exist here, but *Vaccinium* is typically an upland plant, requiring good drainage, which may account for its paucity on Soay. *Nardetum* is not represented on the island, only an occasional plant of *Nardus* being found. The reasons for its absence are not evident, but there is little *Nardetum* on neighbouring islands. *Eriophoretum* is absent, which is not surprising since in extensive areas of moorland quoted by Fraser in Western Scotland *Trichophoretum* appears to replace it.

In comparison with Canna there is a general similarity, though the drier communities dominated by *Calluna*, *Molinia* and *Trichophorum* are less extensive on Soay, while the wetter *Trichophorum* and *Sphagnum* communities are more widespread. The absence of *Vaccinium myrtillus* and *Myrica gale* from Canna is noteworthy, and the augmenting of communities by species from grassland has already been mentioned. The most distinctive feature of Soay vegetation in comparison with Canna and neighbouring islands is the well-developed woodland, this probably being caused by greater protection from winds. Lack of regeneration and the unhealthy conditions of many trees show, however, that conditions are not entirely favourable.

ACKNOWLEDGMENTS.

I should like to thank the Natural History Museum, South Kensington, for confirming the identification of some vascular species; Mr. A. H. Norkett in particular for the identification of the bryophytes; Dr. M. G. Calder for her encouragement; and the Central Research Fund of the University of London for the grant which partly financed the work. Finally, my thanks are very gratefully given to Dr. J. M. Lambert for her valuable help and criticism in the writing of this paper.

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A NOTE ON THE BEHAVIOUR OF *AMMOPHILA ARENARIA* (L.)
LINK. IN RELATION TO SAND-DUNE FORMATION.

By A. R. GEMMELL and P. GREIG-SMITH, late of Victoria University,
Manchester; and C. H. GIMINGHAM, University of Aberdeen.

(Read by title, 15th January 1953.)

An account of the mode of formation of tussocks of *Ammophila arenaria* in mobile dunes, based on observations at Luskentyre, Isle of Harris, Outer Hebrides, has been given previously (Greig-Smith *et al.*, 1947). It was shown that tussocks arise by the local aggregation of leafy shoots (vertical shoots with short internodes and foliage leaves), resulting from their mode of production from horizontal rhizomes. Internode length varies cyclically along the horizontal rhizomes. Only a comparatively small proportion of buds on the horizontal rhizome give rise to leafy shoots, and the latter are produced more frequently from nodes in regions of maximum internode length, commonly on a number of adjacent nodes.

Further work at Luskentyre, supplemented by observations elsewhere, especially at Ainsdale dunes, Lancashire, has made it possible to amplify the earlier account and to correct some points of detail. In view of the indefinite postponement of a detailed study of the ecology of *A. arenaria*, it seems worth while to place these additional observations on record, although there are still points which require further investigation.

The environment and vegetation of the Luskentyre dunes have been described elsewhere (Greig-Smith *et al.*, 1947; Gimingham *et al.*, 1948), and it is sufficient here to note that they form an actively growing dune system on very highly calcareous sand, with comparatively little erosion and subject to little interference other than very slight grazing. Ainsdale dunes form a more stable system, now showing little tendency to extend seaward, but with much erosion in the older dunes, and subject to considerable trampling. The sand has a much lower carbonate content than that at Luskentyre and in the older dunes free carbonate is almost lacking (Salisbury, 1925).

Establishment of *A. arenaria* takes place on the foreshore above high-water mark either by seedlings (text-figs. 2a and 1a), or by

regeneration from pieces of rhizome (text-figs. 2b and 1b) carried down from eroding faces in the established dunes. The previous account implied that seedling establishment predominated. Certainly at Luskentyre in 1946, when the earlier observations were made, seedlings were numerous. In 1947, however, seedlings were almost



TEXT-FIG. 1.—1a, seedling plant of *Ammophila arenaria*; 1b, regenerating rhizome of *A. arenaria*; 1c, length of rhizome showing aggregation of leafy shoots; 1d, top of a vertical rhizome showing much-branched leafy growth.

absent. Search at Ainsdale in the succeeding years has revealed very few seedlings, although pieces of regenerating rhizome are not uncommon. It appears, therefore, that successful establishment of seedlings is sporadic only and perhaps depends on weather conditions which do not occur every year.

Whichever mode of establishment occurs, subsequent development is similar. One, or sometimes more than one, horizontal rhizome is produced (text-fig. 2c), either from a seedling or from a

leafy shoot derived from a dormant bud on a piece of old rhizome. Along these horizontal rhizomes leafy shoots arise, localised in the manner described (text-fig. 1c) (Greig-Smith *et al.*, 1947). Sand accumulates around the leafy shoots and the general sand surface is raised, forming an embryo dune (text-fig. 2d and e). At this stage the individual leafy shoots are small and generally unbranched, so that, although they are localised on the dune surface, the aggrega-



TEXT-FIG. 2.—Diagrammatic representation of the mode of origin of a sand-dune system caused by the growth of *Ammophila arenaria*. (For explanation, see text.)

tions of leafy shoots are not sufficiently dense to cause differential sand accumulation and the surface of the dune is even.

At this stage a different mode of growth becomes apparent, involving a third shoot type. The leafy shoots are capable of growing up through a moderate thickness of sand by elongation of individual leaves. If, however, a leafy shoot is overwhelmed by sand, one or more of the axillary buds develops to form a vertical shoot or shoots with long internodes and scale leaves, a type which may be referred to as a *vertical rhizome* (text-fig. 1d). Growth of

the vertical rhizome continues until the surface is reached, when the apex becomes transformed into a new leafy shoot (text-fig. 2f). Apart from its orientation, the vertical rhizome is comparable with the horizontal rhizome.* On a dune where sand accumulation is rapid a new crop of leafy shoots is thus produced, retaining broadly the same pattern as the original ones borne on horizontal rhizomes. Adventitious roots are produced from the nodes of the vertical rhizomes and the horizontal rhizomes soon die, so that the vertical rhizomes become independent of one another (text-fig. 2g). This process may be repeated indefinitely, as long as sand accumulation continues, and it is often possible to see exposed on eroded faces of old dunes the remains of successive segments of vertical rhizomes and the intervening leafy shoots.

As has already been pointed out (Greig-Smith *et al.*, 1947), in the older dunes at Luskentyre dome-shaped tussocks of *A. arenaria* appear, a development correlated with the entry of other species and stabilisation of the sand surface. At Ainsdale, tussocking, though not so pronounced, is evident where other vegetation is still poorly developed. The formation of these markedly raised tussocks, though perhaps emphasised by stabilisation of the sand surface, appears to be due primarily to the behaviour of *A. arenaria* itself. Successive "generations" of leafy shoots on vertical rhizome systems are more vigorous, until on the tops of higher dunes they are quite profusely branched with a large number of leaves. Moreover, one leafy shoot occasionally produces more than one vertical rhizome, each of which gives rise to a new leafy shoot, so that the number of leafy shoots in a group is increased. In these ways the density of leaves in a group of leafy shoots becomes progressively greater and the contrast in "sand accumulating potential" between groups of leafy shoots and the intervening areas therefore also increases.

The final stage is one of degeneration of the tussocks. The latter break down, and short horizontal rhizomes are produced from the vertical rhizomes.† Small leafy shoots, similar to those of the initial phase, arise from the horizontal rhizomes and appear scattered in the turf of the fixed dunes. This degeneration of the tussocks is correlated with the establishment of a closed community of other

* It is beyond the scope of the present note to discuss the cause of the difference in geotropic response. It is clearly correlated with the presence of actively photosynthesising leaves. This is emphasised by the behaviour of horizontal rhizomes which, if no leafy shoots are produced from them, eventually turn up and grow vertically.

† The conditions under which horizontal rhizomes arise from vertical rhizome systems require further investigation. At Ainsdale, in 1951, occasional actively growing horizontal rhizomes were found on comparatively young building dunes.

species and with the cessation of sand accumulation. It is not clear whether the degeneration of *Ammophila* tussocks is the cause or the effect of the correlated changes, *i.e.* whether *A. arenaria* becomes senescent, or responds to a change to a less favourable environment. It is possible that a sudden influx of sand might result in a repetition of the whole cycle, in the manner known to occur in a number of communities (*cf.* Watt, 1947).

ACKNOWLEDGMENTS.

It gives us great pleasure to express our thanks to the following: The Ernest and Evelyn Weiss Botanical Travel Fund of the University of Manchester, and the University of Aberdeen, for financial assistance for the work in Harris; Miss B. Whinfield for assistance with the field work in 1947; and various students of the University of Manchester who excavated rhizome systems at Ainsdale in the course of field classes.

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CONTRIBUTIONS TO THE MARITIME ECOLOGY OF ST. CYRUS, KINCARDINESHIRE. PART III. THE SALT-MARSH.

By C. H. GIMINGHAM.

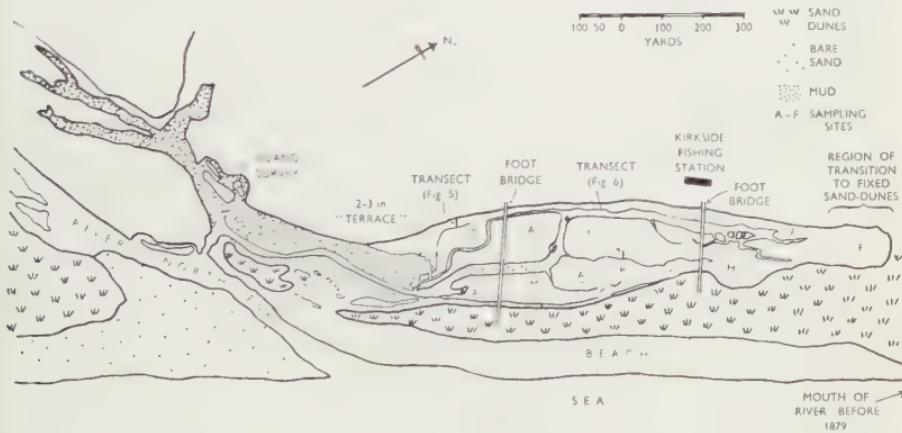
(Department of Botany, University of Aberdeen.)

(With Plate VII.)

(Read by title, 15th January 1953.)

INTRODUCTION.

The previous paper in this series (Robertson and Gimingham, 1951) dealt with the vegetation of the Cliffs (Part I) and the Sand-Dunes (Part II) at St. Cyrus. The present contribution deals with the Salt-Marsh, the third major plant community represented in the



TEXT-FIG. 1.—Map of St. Cyrus Salt-Marsh, 1951.

area under investigation. The salt-marsh is not extensive, covering only about $\frac{1}{8}$ square mile, and occupying a position in the southern half of the bay between a line of cliffs and the sand-dune ridge which runs parallel with the beach. The marsh is long and narrow (text-fig. 1), its long axis running N.E.–S.W., and it connects with the channel of the North Esk a short distance upstream from the river-mouth. It is from this point that the tide fills the marsh. Consequently, the sea water is already diluted to some extent by river water before it enters the marsh, and, as will be shown later, salt

concentrations in the marsh are in general not as high as in some other examples of salt-marshes. A further influence in this direction is the arrival of drainage water from the landward side of the area.

The salt-marsh in its present form is of no great age. Before 1879 the channel of the North Esk followed a course through the area now occupied by the marsh, reaching the sea at a point a short distance north of the present extremity of the marsh. At this date an abnormal spate following a severe snow-storm caused the river to break out at the bend where it turned northwards, thus forming the present mouth. The original mouth was closed by blown sand, and the old course, filled and emptied at each tide from the point of junction with the new channel, developed into a salt-marsh which has therefore been in existence for little more than seventy years. A layer of plant-remains about two feet below the present silt-level in some parts of the marsh may represent the former river-side vegetation.

Change is still to be observed in the plant communities of the marsh, and the loss of two species during its history is of particular interest. There is no longer any trace of *Zostera marina*, which was recorded by Traill from the "old mouth of the North Esk" and must have been present there until about 1920 or later. *Salicornia herbacea* survived longer, being observed in the marsh as late as 1935, but now appears to have been eliminated, although a wide area of uncolonised sandy mud remains at the lower end of the marsh. *Salicornia* has died out or decreased in other places along the north-east coast, and it seems possible that the disappearance of both these species may be linked with increasing amounts of sand in the deposits.

THE HABITAT FACTORS.

(a) *Tides and Submergence.*

The greater part of the salt-marsh is submerged for a time by the majority of tides, except those at the period of Neaps. The full extent of flooding, however, occurs only at high spring tides, when the whole basin is submerged and water reaches to the edge of the sand-hills on either side, and extends well into the transitional region between marsh and fixed dune at the northern extremity. There is little change in level on passing up the marsh, but the centre portion has a slightly convex profile, rising between the two chief drainage channels. This has an effect on the duration of submergence in the central area.

(b) *Edaphic Factors.*

(i) *Physical.*—Profiles exposed at various parts of the marsh consistently show a single layer of dark mud varying between 6 inches and about 14 inches in depth, overlying sand. This suggests that after the river course was altered, the old bed of the river was extensively covered with sand blown from the dunes before silting and salt-marsh development began. The upper mud itself contains a fair proportion of sand, especially at the margins and northern extremity where the basin is fringed by sand-hills, but as yet there is no sign of alternating layers of mud and sand * described from other salt-marshes occurring in the proximity of dunes (e.g. Scolt Head, Steers, 1934).

In some places at the upper end of the marsh a horizon of gravel was found at a depth of about 2 feet below the surface. This may represent part of the old river-bed.

(ii) *Analytical.*—Samples for analysis were taken at weekly intervals throughout a year from six fixed sites. These are shown by letters on the map (text-fig. 1). Sites A, B and D are at the edges of the marsh, C is in the very centre, E is close to a large stand of *Scirpus maritimus* (see p. 157), and F is in the transitional region between the salt-marsh and fixed sand-dunes. The samples, taken at a depth of from 1 to 4 inches, were analysed for pH, total water content and salinity, and a summary of the results obtained is given in Table I.

TABLE I.

ANALYSIS OF SOIL SAMPLES TAKEN WEEKLY THROUGHOUT 1949.

Site.	pH.		Water Content (% of oven-dry wt.).		Salinity (% NaCl in soil water).	
	Mean.	Range.	Mean.	Range.	Mean.	Range.
A	7.18	6.41-8.71	29.9	0.9-94.9	1.56	0.03-8.34
B	6.71	6.03-7.86	90.9	2.0-201.1	1.16	0.03-4.98
C	6.80	6.28-7.39	169.0	13.3-416.0	0.92	0.04-3.89
D	6.89	6.11-8.02	91.4	13.4-187.2	1.17	0.03-5.08
E	6.75	6.10-7.46	151.4	22.3-348.4	0.67	0.06-1.69
F	6.79	5.80-7.65	44.8	5.1-159.1	0.60	0.04-2.19

* Except in one spot at the eastern edge of the lower end of the marsh where a $4\frac{1}{2}$ -inch layer of sand overlies a dark muddy horizon of $1\frac{1}{4}$ inches, below which is sand again.

Acidity. pH was measured electrometrically, using a glass electrode. There is little significant variation in the acidity of the samples, either with time of year or position on the marsh. Site A, at the edge of the lower end of the marsh where the samples contain a high proportion of sand, differs slightly from the rest in giving a mean pH of just over seven. The great majority of samples at the remaining sites are on the acid side of neutrality, but the only situation in which pH values lower than six occur is F, bordering the fixed sand-dunes where an appreciable amount of organic material is incorporated in the soil. Elsewhere the proportion of organic material is low.

Water content varies greatly according to the date and time of sampling in relation to the state of the tides. The figures in Table I (obtained by oven-drying the samples to constant weight at 100° C.) show, however, that water retention is least at the sides and upper end of the basin; here the marsh borders the sand-hills and the higher proportion of sand in the soil permits more efficient vertical drainage. The lowest mean value is found at A, where no values higher than 95 per cent. are recorded even immediately after submergence, and the soil readily dries out during periods of exposure. In the central regions of the marsh the mud never dries out to such an extent, and the highest mean is reached in the centre (C) where very high values are sometimes obtained—probably owing to the difficulty of draining off standing water from samples of the mud. Very high levels of moisture are also obtained at E, close to the *Scirpus maritimus* colony, to which further reference is made later.

Salinity. The sea water in St. Cyrus bay has a chloride concentration equivalent to a solution of about 3.0 per cent. NaCl, but that of the flood water covering the marsh is usually rather lower. Samples taken from pools of water standing at the lower end of the marsh after a period of tidal exposure gave concentrations equivalent to 2.5 per cent. NaCl. The salinity of the solution in contact with plant roots depends partly on that of the water flowing over the marsh, partly on evaporation, and partly on dilution by rain and the inflow of fresh water from landward sources. It was estimated by extracting air-dried samples with distilled water and titrating with standard silver nitrate solution, expressing the result in terms of NaCl. Owing to the variations in the water content of the soil, figures indicating amounts of salt per unit weight of dry soil would be meaningless. When expressed, however, as % NaCl in soil water as in Table I, an indication of salinity as it affects the vegeta-

tion is obtained. The lower levels of salinity show little variation, presumably representing conditions reached anywhere on the marsh after rainfall, but there is a general increase in the mean and maximum levels on passing towards the lower end of the marsh, which is submerged more frequently and for longer periods. The fact that site C in the centre of the marsh shows lower values than D may perhaps be explained by the convexity of the central part of the marsh, resulting in shorter periods of submergence than in certain areas towards the sides.

VEGETATION.

Methods. Analysis of the vegetation was carried out along the following lines:

1. The general pattern of the vegetation over the area was obtained by determining the frequencies of the various species at intervals along representative transects. A quadrat measuring 1 square metre was divided into a grid of 36 equal squares. At each position on a transect this quadrat was placed eight times at random within a small area and the species present in every alternate small square of the grid were recorded. Thus the frequency of each species in 144 samples of $\frac{1}{36}$ square metre was recorded.
2. Sketch-maps were made of the distribution of each of the more important species, in relation to the various fixed points, such as drainage channels, bridges, etc.
3. A detailed quantitative analysis was made of a small area containing most of the species belonging to the salt-marsh flora. The area selected was an island, completely surrounded by channels (text-fig. 1). A horizontal base-line was laid down the centre, and offsets were run at regular intervals. At every foot along these offsets the plants occurring at two points, 2 inches apart, were recorded, and the position levelled relative to the base-line. At regular intervals soil samples were collected for estimation of moisture and salt content.
4. The most prominent species in the flora were investigated from an autecological standpoint.

General Aspects of Succession.

The lower third of the basin consists mainly of bare sandy mud, devoid of colonising plants, except for scattered patches of algae. Detailed algal studies have not been included in the present survey,

but *Fucus ceranoides* is prominent on stony regions near the drainage channels, and the scattered green algal films include species of *Ulva*, *Enteromorpha* and *Vaucheria*.

The junction between the part of the marsh carrying vegetational cover and the bare portion is marked by a small terrace edge, about 2-3 inches in depth. Immediately below this "step" there is generally a fringing algal mat composed chiefly of *Vaucheria*, while *Enteromorpha* occupies the terrace edge itself. The pioneer species is *Puccinellia (Glyceria) maritima* alone. The presence of the "step" suggests that downward extension of the communities has not proceeded for some while, and perhaps a certain amount of tidal erosion has taken place. There are, however, isolated plants of *Puccinellia* occurring fairly frequently in the algal mat below the "step", perhaps representing some renewal of colonisation.

The lower limit of fully developed salt-marsh vegetation, as marked by the "step", does not form a straight boundary across the basin, but extends towards the bare mud in a series of tongues and partially disconnected islands with channels between them. The community in this region is dominated by low-growing *Puccinellia maritima*, and contains a high proportion of *Aster tripolium* and numerous large tussocks of *Triglochin maritima*, with scattered *Atriplex babingtonii*. The structure of the community even at this lower limit of salt-marsh vegetation suggests that it has already been preceded by successive stages of development.

A dense algal mat, composed of species of the genera *Enteromorpha*, *Vaucheria* and *Rhizoclonium*, covers the mud surface among the shoots of *Puccinellia*, especially in the wettest regions, becoming less conspicuous on passing up the marsh. *Enteromorpha* is abundant only in the lower part and by the channels, becoming less frequent on passing away from a constant supply of more or less saline water. *Vaucheria* and *Rhizoclonium* are widespread, but tend to replace each other (text-fig. 5), the former being prominent close to the channels and in permanently saturated situations, giving place to the latter as distance from standing water increases. Carter (1933) regards these three genera as the most widespread on salt-marshes and also notes that *Vaucheria* becomes dominant locally in the slightly moister spots.

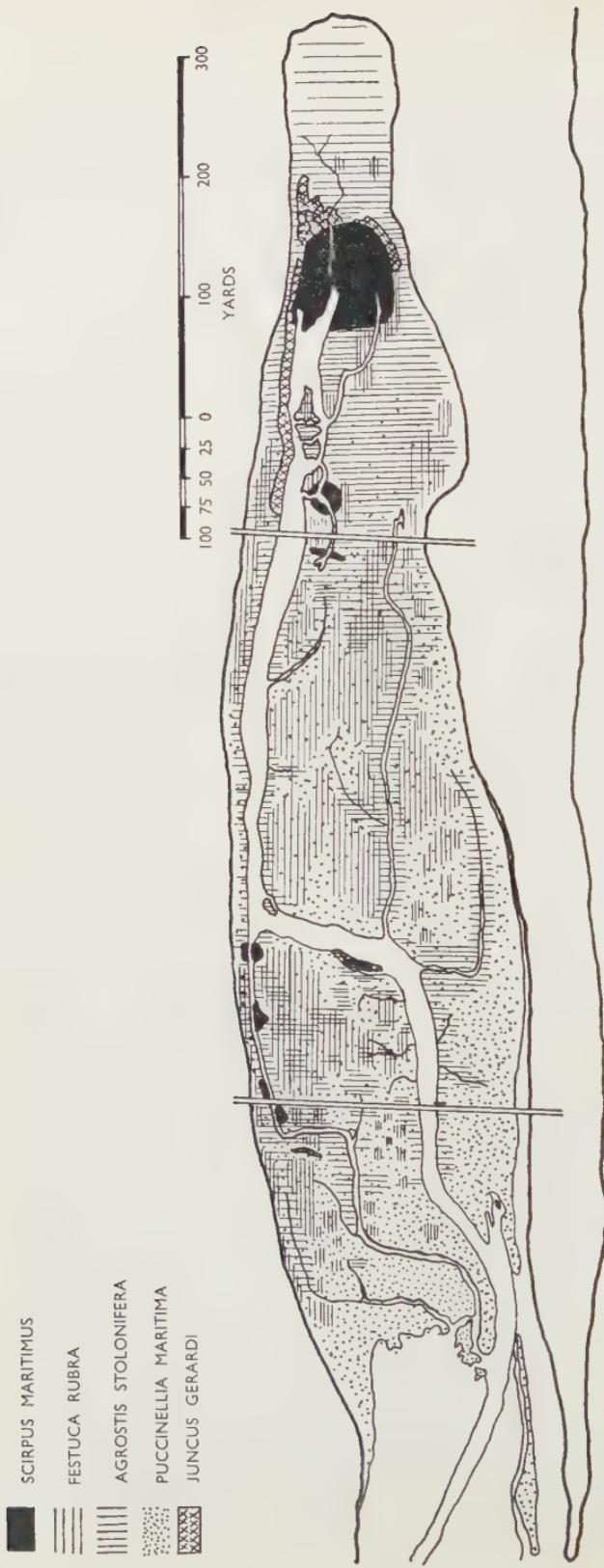
Owing to the shape of the marsh and the complexity of the drainage system there is no clear zonation of communities, and changes in the community composition are not easy to recognise. The drift in the representation of different species along the transects passing up the main central part of the basin, however, probably represents

the direction of the plant succession associated with increase in silting and the reaction of plants upon the habitat. *Puccinellia maritima* is prominent over the greater part of the marsh except at the edges and the northern extremity. On passing towards the middle part of the basin the associates mentioned above tend to become less numerous, while *Cochlearia officinalis*, *Plantago maritima* and *Glaux maritima* increase.

In many other salt-marshes described in the literature a community dominated by *Limonium vulgare*, *Armeria maritima* or *Obione (Atriplex) portulacoides*, or some combination of these, develops at this stage. *Armeria maritima*—the only one of these species present at St. Cyrus—is, however, here restricted to a zone fringing the edge of the marsh (p. 147), and there is direct invasion of the *Puccinellia* communities by *Festuca rubra*. This species extends its dominance well into the lower half of the marsh, especially in the central portions between the main channels (text-fig. 2). Its prominent rôle is paralleled in other marshes characterised by a sandy soil. There is evidence to suggest that it is actively extending its area towards the lower end of the marsh, although considerable enclaves dominated by *Puccinellia* remain even well up in the upper half. *Cochlearia officinalis*, *Plantago maritima*, and to a lesser extent *Glaux maritima* and *Aster tripolium* remain as characteristic associates in the Festucetum.

Certain portions of the upper part of the marsh, in particular its northern extremity, appear to lie at a slightly lower level than the greater part of the Festucetum. Here the mud is rather deeper and freer of sand, and in these very wet regions *Agrostis stolonifera* becomes dominant in place of *Festuca rubra*, extending its area downwards along the more or less permanently wet margins of the channels. A large circular area near the upper end of the marsh maintains water-logged conditions even more effectively and supports an extensive and dense stand of *Scirpus maritimus*, while similar small areas farther down the marsh are also becoming occupied by *Scirpus* (text-fig. 2). *Triglochin maritima* appears to be associated with a saturated substratum; in addition to its area at the lower end of the marsh, it occurs abundantly around the *Scirpus* areas and in various places on the edges of channels (text-fig. 4). Another associate in such conditions is *Atriplex babingtonii*, which is found regularly amongst *Agrostis* and especially with the *Scirpus*.

The remaining community represented in the main part of the marsh is one dominated by *Juncus gerardi*. This occurs as a fringe round the northern and western edges of the large *Scirpus* community



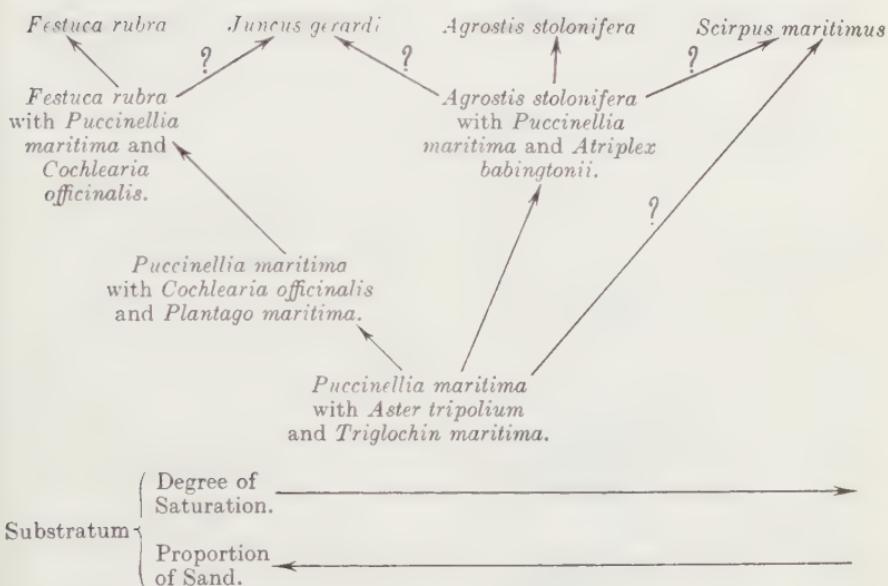
TEXT-FIG. 2.—Approximate distribution of *Scirpus maritimus*, *Festuca rubra*, *Agrostis stolonifera*, *Puccinellia (Glyceria) maritima*, and *Juncus gerardi* on St. Cyrus Salt Marsh, 1951.

(text-fig. 2). It appears to be expanding its area, enclosing enclaves of *Agrostis stolonifera*, while towards the sides of the basin it abuts on communities typical of the edges of the marsh.

The distribution of these communities imposes considerable uncertainty in identifying the successional developments. The scheme outlined in Table II, however, is tentatively suggested.

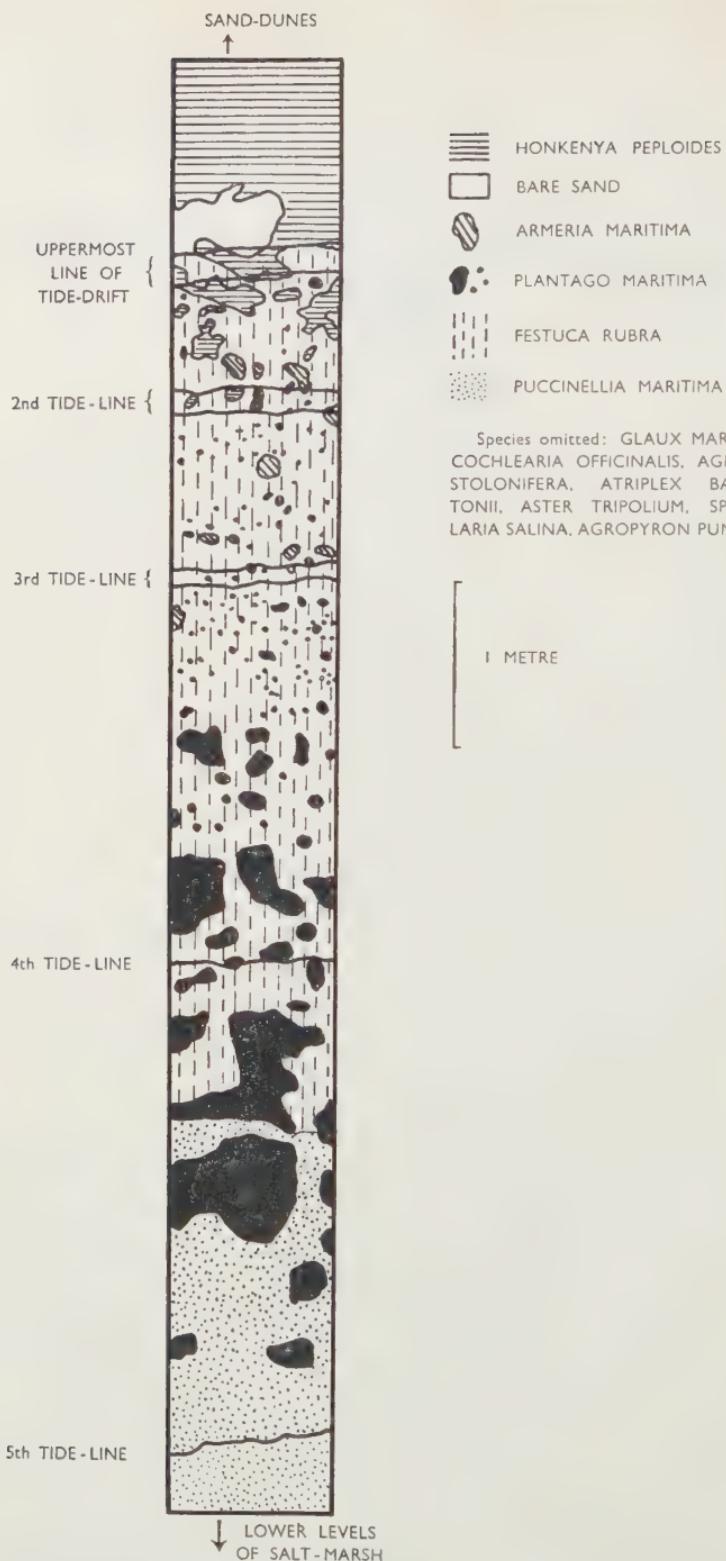
TABLE II.

SUCCESSIONAL DEVELOPMENT.



Zonation at Edges of Salt-Marsh.

At the edges of the marsh, where it passes fairly abruptly into sand-hills, a distinct zonation may be traced, resulting from the effects of the upward slope upon frequency and duration of submergence, and from increasing proportions of sand in the soil. At periods of spring tides, clear lines of tide-drift indicate the limits of occasional submergence (text-fig. 3). Above the highest line of drift, *i.e.* in regions never submerged or possibly covered very occasionally by the highest spring tides, the sand is occupied by species such as *Carex arenaria*, or in certain areas by a dense mass of *Honkenya (Arenaria) peploides* which seems to find favourable conditions in such situations. Below the highest drift line, *i.e.* in regions submerged once or a few times each month, the community



TEXT-FIG. 3.—Plan of belt transect showing zonation at edges of salt-marsh.

becomes dominated by *Festuca rubra*, with *Armeria maritima* abundant at this upper level. *Honkenya peploides* decreases, and is altogether absent below the second line of drift. Below the third line, where vegetation is presumably submerged several times each month, *Armeria* disappears and *Plantago maritima* enters, first as scattered small plants, increasing in size on passing downwards, and at the lower levels merged in large clumps. In other parts, *Plantago maritima* may extend up as far as the upper line of drift.

The exact nature of the zonation varies according to position in the basin, but its general features remain constant. In the lower part of the marsh, the *Festuca* zone gives place on passing inwards to *Puccinellia maritima*, where submergence is more regular. *Glaux maritima* is a constant feature throughout the zonation, reaching to just above the upper limit of drift, while *Cochlearia officinalis*, also constant throughout, reaches well above this limit.

The relative arrangements of these species reflect their varying ecological amplitudes, which are discussed more fully in a later section.

Other species found less abundantly on the sandy fringes of the marsh in the regions occasionally submerged by high spring tides include *Agropyron pungens*, which is very localised and has been found only on the western side; *Sagina maritima* (abundant); *Atriplex babingtonii* (frequent); *Plantago coronopus* (frequent); and *Spergularia salina* (occasional). The last species occurs also at the lower end of the main part of the marsh amongst *Puccinellia maritima*, but appears to be largely replaced by *Spergularia marginata* amongst the taller and denser vegetation of the central regions. There seems, however, to be some overlap in the distributions of the two species.

Transition to Fixed Sand-dunes at Apex of Salt-Marsh.

The northern extremity of the basin shows features similar to the zonation at the sides, but the transition is more gradual. A much wider belt dominated by *Armeria maritima** is present, passing into an area of scattered hummocks occupied by sand-dune communities, between which there is normally a considerable accumulation of tide-drift. The flora of this region includes a

* The prominence of *Armeria* here and in the belt round the edges of the marsh is probably related to the high proportion of sand in the soils of these areas, as suggested by Marsh (1915).

number of species not otherwise belonging to the salt-marsh communities:

ATRIPLEX BABINGTONII	.	.	a	ARMERIA MARITIMA	.	.	.	f
SONCHUS ASPER	.	.	a	GALIUM APARINE *	.	.	.	f
PLANTAGO CORONOPUS f. PYGMAEA*	a			GLAUX MARITIMA	.	.	.	o
SAGINA MARITIMA *	.	.	a	PLANTAGO MARITIMA	.	.	.	o
RUMEX CRISPUS	.	.	f-a	COCHLEARIA OFFICINALIS	.	.	.	o
POTENTILLA ANSERINA *	.	.	la	SYMPHYTUM OFFICINALE	.	.	.	o
AGROSTIS STOLONIFERA	.	.	f	CIRSIUM ARVENSE	.	.	.	o
FESTUCA RUBRA	.	.	f	CAREX OTRUBAE (VULPINA)*	.	.	r	
PUCCINELLIA MARITIMA	.	.	f	MELANDRIUM RUBRUM	.	.	r	
AMMOPHILA ARENARIA	.	.	f					

The majority of species in this flora are characteristic either of the sand-dunes or of the salt-marsh and occur mixed in the transitional region, but those marked with an asterisk (*) appear to belong particularly to this habitat.

AUTECOLOGICAL ASPECTS OF PROMINENT SPECIES.

The following observations on the ecological amplitudes of various species and their interactions are based upon intensive studies of each species, together with results of the examination of transects in different parts of the marsh and a detailed quantitative study of a small "island" containing most of the plants mentioned.

The Grasses.—The general distribution of *Puccinellia maritima*, *Festuca rubra* and *Agrostis stolonifera* in the salt-marsh area is illustrated in text-fig. 2.

Puccinellia maritima has a very widespread distribution over the marsh, except at the northern extremity and locally where it is excluded by dense stands of *Festuca rubra*, *Agrostis stolonifera* or *Scirpus maritimus*. As in the case of *Agropyron junceum* in the sand-dune succession,† isolated colonising plants of *Puccinellia maritima* adopt the form of a small rosette with the leafy shoots closely appressed to the mud. This growth-form is probably associated with establishment of the species in the early stages of succession, and as the colonies develop and the plant becomes dominant at the lower end of the marsh it remains low-growing, with many shoots prostrate or oblique. Later, as the community becomes denser and the level of the substratum rises, the shoots adopt a more erect habit,‡ and by this time the other grass species may be found

† See Part II of this series, vol. xxxv, p. 396.

‡ This change in growth-form was also recorded by Yapp and Johns (1917) on the Dovey marshes.

growing in association with *Puccinellia*. In spite of its wide general range, a definite association of *Puccinellia* with the lower levels has been shown in the detailed survey of the "island".

The distribution of *Puccinellia* is closely related to high water content in the substratum, and its region of dominance coincides with the more saline part of the marsh. Owing to the width of its range, however, the latter effect probably results from the inability of other species to compete under these conditions rather than from any stimulatory effect upon *Puccinellia*. These conclusions are borne out by the fact that in the higher parts of the marsh *Puccinellia* is abundant only in the proximity of channels (text-figs. 2 and 6).

The status of *Festuca rubra* is of interest, since it appears to be actively extending its area. It is not as widespread as *Puccinellia*, but takes the place of the latter in the drier areas of the upper and western parts of the marsh, being replaced in the wetter regions by *Agrostis stolonifera*.

Festuca rubra is absent from the wettest and most saline parts of the marsh. In Table I, for example, the sampling sites at which *Festuca* is dominant are B and D, while text-figs. 2, 5 and 6 show that in the central parts of the marsh it does not enter into the communities close to the channels, but becomes dominant in large patches between the major drainage channels where a higher level reduces both water content and salinity. It is particularly conspicuous in these areas in late June and July, when the dense stands of inflorescences mark the positions in which it is abundant.

Evidence indicating spread of *Festuca rubra* both eastwards and towards the lower end of the marsh has been obtained. The map (text-fig. 2) demonstrates the large number of isolated patches of *Festuca* in the lower part, which show all the characteristics of new colonising centres. One of these, towards the eastern side of the marsh, was marked in 1948 and increased its diameter by more than 2 feet in certain directions during the succeeding year and has continued to expand.

It follows that in many parts of the marsh *Festuca* and *Puccinellia* are present together. In certain areas in the lower parts *Festuca* is only just able to persist, but elsewhere, after establishment, it begins to gain dominance over *Puccinellia*. The inverse relations between the number of shoots of *Festuca* and the number of shoots of *Puccinellia*, and its inhibiting influence on the production of inflorescences by *Puccinellia*, are shown in Table III. (A metre quadrat grid of 36 equal squares was used and the shoots occurring

at each of the 25 intersections of the grid were scored. Four quadrats are selected from a transect.)

TABLE III.

RELATIONSHIP BETWEEN NUMBERS OF SHOOTS OF *FESTUCA RUBRA*
AND *PUCCINELLIA MARITIMA*.

Quadrat No.	Number of Shoots of <i>Festuca rubra</i> .	Number of Shoots of <i>Puccinellia maritima</i> .	
		Total.	Flowering.
28	0	23	23
29	17	4	0
30	2	21	12
31	23	0	0

It also appears that the vigour of *Puccinellia* is reduced when growing in competition with *Festuca*, since its general height when growing alone is 18–20 inches, while in company with *Festuca* it is usually only 14–16 inches.

The third species, *Agrostis stolonifera*, appears sometimes in association with the other two, either singly or together, but it is favoured by different conditions and tends to become dominant in dense pure colonies. It is dominant over an extensive part of the upper end of the marsh, more locally in the central regions, and towards the lower parts along the banks of channels. The conditions which these situations have in common are that, while they are low in salt content, they are constantly among the wettest areas of the marsh, retaining standing water for long periods. Thus, in Table I, *Agrostis* is dominant at sites C (with *Puccinellia*) and E, while the area in which it is densest is around and below the large *Scirpus* patch which has been shown to occupy the wettest part of the marsh. *Agrostis* is also prominent close to the smaller colonies of *Scirpus*.

Counts of shoots of *Agrostis stolonifera* and *Festuca rubra* at the intersections of a grid placed in situations selected in the higher and dryer parts of the marsh (A), as compared with others in more low-lying and wetter parts (B), demonstrate the respective preferences of the two species (Table IV).

In the central part of the marsh the patches of *Agrostis stolonifera* appear to be wetter than neighbouring areas dominated by *Festuca*

TABLE IV.

EFFECT OF HABITAT UPON THE PROPORTIONS OF *FESTUCA RUBRA*
AND *AGROSTIS STOLONIFERA*.

Situation of Quadrat.	Number of Shoots of <i>Festuca rubra</i> .	Number of Shoots of <i>Agrostis stolonifera</i> .
(A) 1	11	0
	23	0
	21	0
(B) 1	0	21
	0	17

rubra. Examination of a number of profiles dug in this region showed that *Agrostis* (sometimes in association with *Puccinellia*) occupies situations where the mud layer is deepest; others in which the mud layer is only about 10–11 inches deep, overlying sand, are occupied by *Festuca rubra*. Further, comparable pairs of samples of the top 3 inches of mud taken at the same time from nearby areas of *Agrostis* and *Festuca* gave the values for water content shown in Table V.

TABLE V.

PER CENT. WATER CONTENT IN MUD FROM *AGROSTIDETUM*
AND *FESTUCETUM*.

	<i>Agrostis stolonifera</i> .	<i>Festuca rubra</i> .
Pair 1 . .	187.5	164.5
Pair 2 . .	171.9	156.0
Pair 3 . .	213.7	169.0

Text-figs. 2 and 5 illustrate the fact that *Agrostis* is extending its area of dominance into the lower parts of the marsh, but in this region it is clearly restricted to narrow belts along the sides of channels. This again indicates that a high water content in the

substratum is among its requirements, since, as shown in text-fig. 5, water content is highest in the *Agrostis* belt, falling as distance from the channel increases.

As with *Festuca* and *Puccinellia*, it appears that where *Festuca* and *Agrostis* occur together in situations favouring the former, it exerts an adverse effect upon the vigour and flowering of its associate (Table VI; figures obtained as for Table II).

TABLE VI.

RELATIONSHIP BETWEEN NUMBERS OF SHOOTS OF FESTUCA
RUBRA AND AGROSTIS STOLONIFERA.

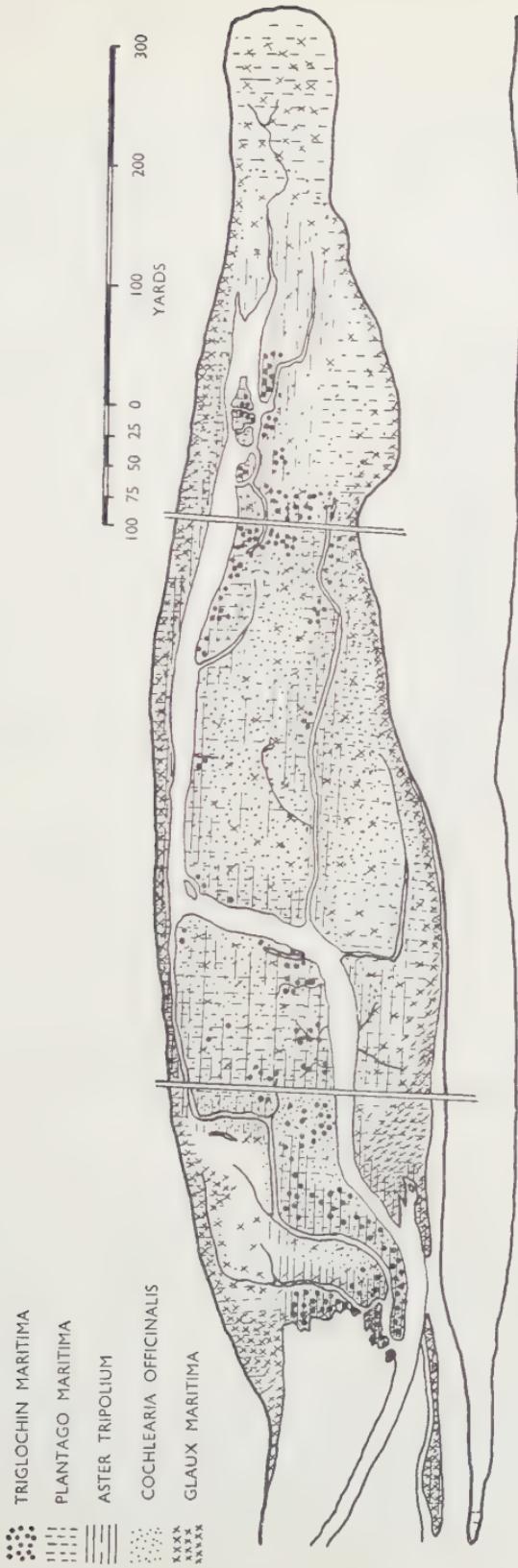
Quadrat No.	Number of Shoots of <i>Festuca rubra</i> .	Number of Shoots of <i>Agrostis stolonifera</i> .	
		Total.	Flowering.
15	21	2	0
17	9	13	2
18	24	0	0

As with *Puccinellia*, the height of *Agrostis* is reduced from 18–21 inches to 13–14 inches when growing with vigorous *Festuca*.

The three species of grasses therefore exhibit slightly overlapping ecological amplitudes, of which that of *Puccinellia* is the widest.

Aster tripolium. The general distribution of *Aster* is shown in text-fig. 4, but its autecology has not been examined in detail. It is the first species to become associated with *Puccinellia maritima* and is frequent at the lower end of the marsh, decreasing on passing upwards except in areas close to channels and in the *Scirpus* community. It is therefore associated with the wetter parts of the marsh (as indicated by Morss (1927) in the Nith Estuary), but never becomes dominant of a zone as in other salt-marshes (e.g. Scott Head, Chapman, 1934).

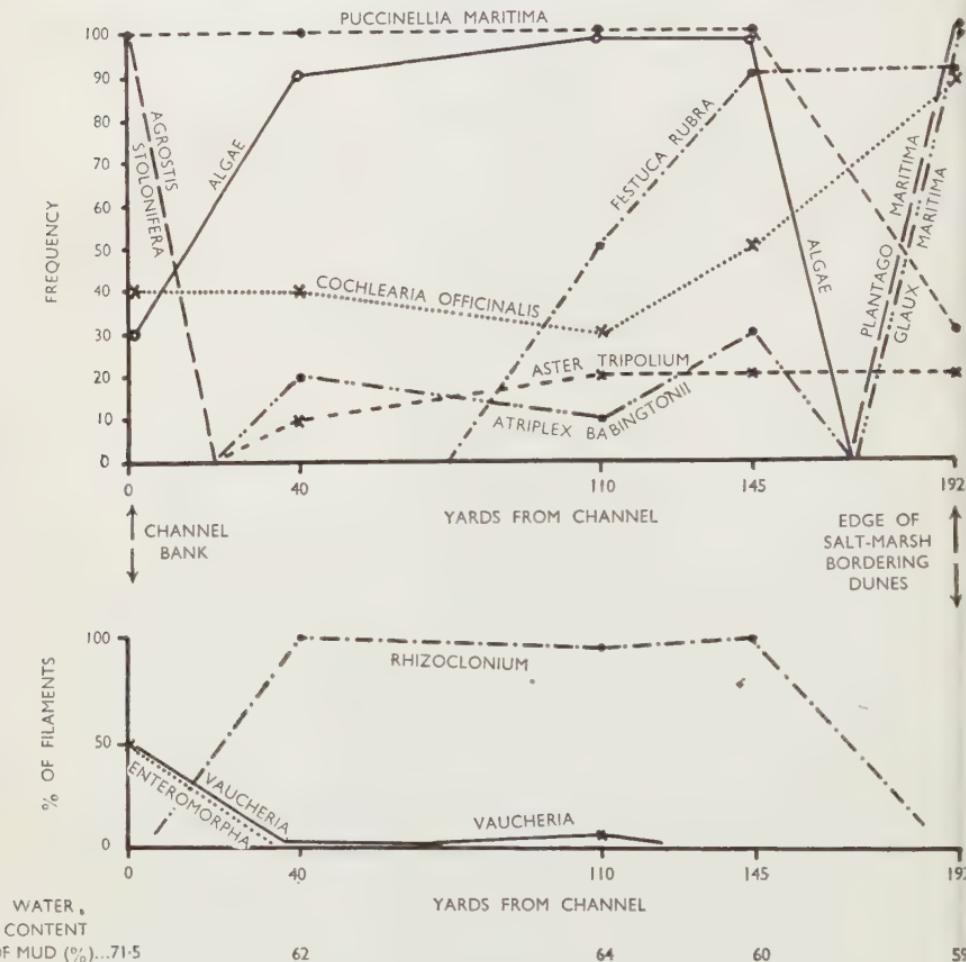
Cochlearia officinalis. This species is very abundant and widespread over the greater part of the marsh (text-fig. 4), entering early at the lower end and becoming numerous in association with *Puccinellia*, and especially so with *Festuca rubra*. The transects, however, show that it is less frequent in the wetter parts, being scarce in the belts close to channels but becoming very prevalent in the rising ground between channels (text-fig. 5). This is in



TEXT-FIG. 4.—Approximate distribution of *Triglochin maritima*, *Plantago maritima*, *Aster tripolium*, *Cochlearia officinalis*, and *Glauca maritima*, on St. Cyrus Salt-Mars, 1951.

accord with the observations that it is sparse in areas dominated by *Agrostis stolonifera* and *Scirpus maritimus*.

Cochlearia ranges from the centre of the marsh up to the edges bordering on to sand-hills, and the width of habitat range is paralleled by a wide range of growth-form. At the edges of the marsh where



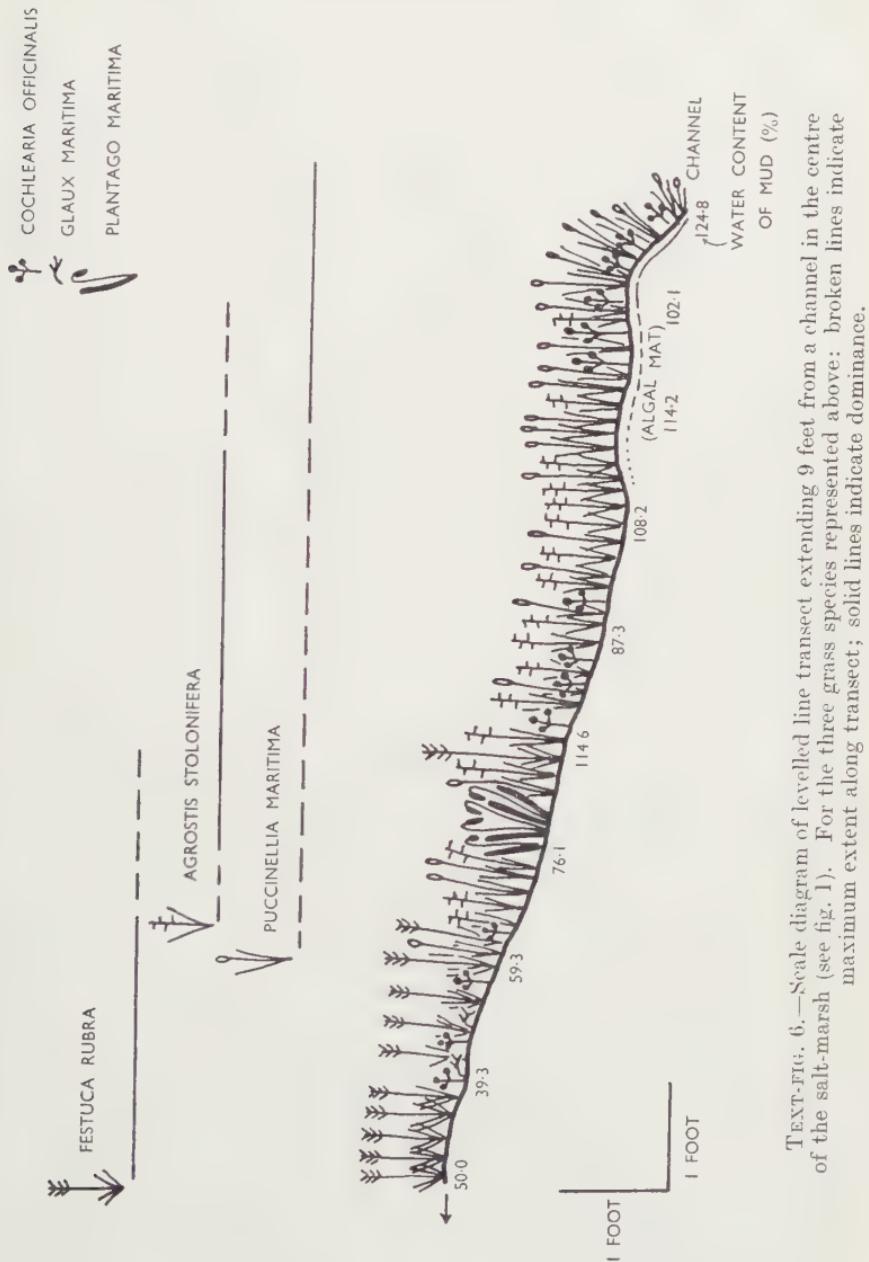
TEXT-FIG. 5.—Transect from the bank of a channel to the edge of the salt-marsh (for location see fig. 1).

Upper diagram: Changes in frequencies of species along transect.

Lower diagram: Changes in the representation of algal genera along transect.

the grazing effect of rabbits is pronounced, *Cochlearia* adopts a small, flat habit. There is every grade of transition between this and the tall, rather straggling plants found amongst *Festuca* in the centre of the marsh. At the time of flowering these plants have few vegetative leaves and the tall inflorescences are largely supported by the

vegetation around them. The form appearing in wetter, more open situations on channel banks provides a contrast in that it



TEXT-FIG. 6.—Scale diagram of levelled line transect extending 9 feet from a channel in the centre of the salt-marsh (see fig. 1). For the three grass species represented above: broken lines indicate maximum extent along transect; solid lines indicate dominance.

has a thick cluster of vegetative leaves from which arise several inflorescences of medium height.

Plantago maritima has a widespread distribution similar to that of

Cochlearia, but it is never so abundant and does not reach the lowest limits of the marsh (text-fig. 4). It therefore enters at a slightly later stage of development than *Cochlearia*, but, like it, is an important component over the whole central part of the marsh. Its association with the dryer and more sandy regions, however, is clear, and it forms a distinct zone of large clumps a short distance below the *Armeria* belt at the edges of the marsh (p. 147). On the "island" it was found to be associated with the higher levels.

As in the case of *Cochlearia*, the growth-form of plants in more or less open situations is compact, tending to a rosette type with a maximum height of about 4 inches, while amongst tall *Festuca*, plants are of a more upright form and up to about 14 inches in height.

The form of *Plantago maritima* with dark spots on the leaves is present together with the normal type. It is particularly numerous in a sandy area at the eastern edge of the lower part of the marsh, where spotted forms constitute 45 per cent. of the total population of the species, whereas outside this area they constitute only 9 per cent. No evidence has been obtained to suggest a cause for such localisation of the spotted form, although a less pronounced concentration of spotted individuals was noted in a similar area on the western edge of the marsh.

Glaux maritima. *Glaux* also enters the community at an early stage at the lower end of the marsh, and has a wide distribution throughout the area (text-fig. 4). It is, however, particularly abundant in the less wet, more freely drained sandy situations at the sides of the lower part of the marsh, and becomes co-dominant with *Puccinellia maritima* in the low-growing, rabbit-grazed community on the sandy spits at the eastern edge of the lower reaches. Site A (Table I) was located in this community and showed fairly high salt concentrations but poorer water retentivity and a sandier substratum than elsewhere. The plants here exhibit a dwarf, prostrate form (maximum height, $1\frac{1}{4}$ inches) with many branches, forming a dominant carpet with relatively few associates which include small *Aster tripolium*, *Cochlearia officinalis*, *Suaeda maritima*, *Spergularia salina*, *Atriplex babingtonii* and *Plantago maritima*. *Glaux* is absent from the belts adjacent to channels (text-fig. 5), entering the community only in the drier regions some distance from the banks. Morss (1927) also noticed that *Glaux* withstands fairly high salt concentrations and is most abundant in "open" soils.

Glaux maritima occurs in all the other communities of the marsh, though less abundantly. Its height varies according to that of the surrounding vegetation, much of the increased stem-length being

achieved by elongation of the internodes. The extreme development is observed amongst *Scirpus maritimus*, where an etiolated form, up to $10\frac{1}{2}$ inches with very few branches, is obtained. *Glaux* flowers most freely in the more open communities of the centre of the lower end of the marsh, where it is neither surrounded by very dense vegetation nor heavily grazed.

Scirpus maritimus. The large, more or less circular area at the northern end of the marsh occupied by a dense stand of *Scirpus*, about $3\frac{1}{2}$ –4 feet tall, has already been mentioned. Smaller patches occur elsewhere (text-fig. 2). In all these areas the run-off of tide water seems to be impeded, perhaps because they represent hollows in the general level. It is certain that they retain a constantly high water content (see Table 1, site E, which was located at the edge of the main *Scirpus* colony), and standing water is frequently observed at times when the surrounding shorter communities are entirely exposed. Each colony is situated at the side of a channel or at the end of a channel branch, and the largest surrounds the ends of the main channels. These regions fill more rapidly with the oncoming tide and drain more slowly than neighbouring areas farther from the channels.

This description of the conditions obtaining is in close agreement with expectation from an examination of the associated species. Algae, especially *Vaucheria* and blue-green algae, are prominent, particularly in the less dense parts, forming a mat over the mud and sometimes coating the lower parts of the *Scirpus* shoots. *Aster tripolium*, *Atriplex babingtonii* and *Cochlearia officinalis* are frequent, except where *Scirpus* densities exceed about 60 shoots per square foot (maximum just over 100 per square foot). In the densest regions, light intensity at ground-level may be reduced to less than 20 per cent. of that in the open.

The gradient of conditions on passing outwards from the *Scirpus* is reflected by the presence of two concentric zones surrounding it. The main colony itself is about 127 feet in radius, covering an area of water-logged mud in which the rhizomes are normally no more than 3 inches deep. The surrounding zones are:

- (1) An *Agrostis stolonifera* belt about 6 feet in width. (At the south-east corner a narrower belt of *Puccinellia maritima* lies between the *Scirpus* and the *Agrostis*.)
- (2) A *Juncus gerardi* belt (incomplete, replaced in parts by *Festuca rubra*) on a more freely drained substratum in which the rhizomes penetrate to depths of more than 8 inches.

Although *Cochlearia officinalis* and *Glaux maritima* occur amongst the *Scirpus*, both are more frequent in these fringing communities, expressing their preference for more freely drained substrata.

Rhizomes of *Scirpus* penetrate outwards into the surrounding belts, producing scattered shoots, decreasing in height with distance from the main colony. These would suggest an advancing front of rhizomes in a "pioneer" phase, but marked areas have shown little or no advance during the last three years.

Triglochin maritima. Although nowhere very numerous, *Triglochin* is prominent in certain parts of the marsh owing to the size and denseness of the circular clumps. It is abundant at the lower end in the areas dominated by *Puccinellia maritima*, and occurs in some numbers in the upper parts by the sides of the smaller tributary channels and around the areas occupied by *Scirpus maritimus* (text-fig. 4). This distribution suggests that its requirements are rather similar to those of *Scirpus* in that it demands almost continuous saturation of the substratum, but that it will also tolerate the rather more saline habitats in the lower reaches. In certain respects its distribution is rather similar to that of *Aster* although it is less widespread, and this conclusion was borne out in the detailed survey of the island.

The development of individual plants of *Triglochin* is different from most other species on the marsh, following the pattern outlined by Watt (1947) for species which colonise on a circular front. The smallest plants observed on the marsh take the form of domes, having a diameter of about 4 inches. The rhizomes radiate outwards from the centre of the clump, lying only just below the surface of the mud. Growth is not rapid or extensive and new shoots are formed by the tip of the sympodial rhizome turning upwards almost immediately in front of the previous terminal shoot. Consequently a very dense, expanding clump is produced (Plate VII, 1).

The clump retains its dome shape until a diameter of about 1 foot is achieved. With further expansion, the shoots in the centre become weak and reach a height of only about 1 foot, while those towards the margin are about 1 foot 8 inches tall. The hummock, therefore, has a distinct dip in the centre, and from this stage onwards the colony shows all four phases defined by Watt, on passing from the exterior to the centre: Pioneer, Building, Mature, Degenerating. Following further expansion of circumference, the shoots in the centre die out altogether, leaving the colony in the form of a ring (Plate VII, 2). The centre becomes colonised by species occurring in the neighbourhood; at the lower end of the marsh these are



1



2

1. *Triglochin maritima*: dome-shaped young plant.

2. *Triglochin maritima*: old plant in the form of a ring, the centre of which is now occupied by *Agrostis stolonifera*, *Cochlearia officinalis*, etc.

generally *Puccinellia maritima*, *Aster tripolium* and *Glaux maritima*, while in the upper parts the more usual entrants are *Agrostis stolonifera*, *Puccinellia maritima*, *Cochlearia officinalis* and *Atriplex babingtonii*. Thus, on any one spot over which *Triglochin* colonises, a cyclical change in the vegetation takes place. At various parts of the marsh, rings of over a yard in diameter occur, of which only the periphery of 8-10 inches is occupied by *Triglochin*, while the central portion is dominated by other species. In only one instance did *Triglochin* itself become established within an old ring. It seems unlikely therefore that *Triglochin* would become dominant in an area of any extent, although Yapp and Johns (1917), describing its development under rather different conditions, mention the coalescence of hummocks to form a tussocky sward.

As the shoots of *Triglochin* stand so much taller than the surrounding vegetation, at least at the lower end of the marsh, the waters of an oncoming or of an ebbing tide swirl round each clump. There is a tendency for a narrow belt round the periphery to become cleared of other vegetation, a condition which may lead to the development of minor drainage channels. The rhizomes of plants at the lower end of the marsh run uniformly horizontally, even in the oldest plants. By contrast, those of plants in the upper parts are directed obliquely upwards at angles of up to 45°. This suggests that the taller and denser vegetation of the upper parts may be causing an increase in the surface level of the substratum, perhaps by accumulation of silt and deposition of their own debris, while such effects have been negligible at the lower end, at least during the lifetime of existing colonies of *Triglochin*.

DISCUSSION.

Chapman (1938) has pointed out that in small salt-marshes largely enclosed by shingle or sand-banks, succession proceeds more rapidly than in large "open" marshes, with a consequent compression of the developmental phases. This probably applies directly to the St. Cyrus marsh, in which the sequence of phases appears to be simplified and telescoped in comparison with those in the majority of published accounts. Mention may be made of the restriction of *Armeria maritima* to the edges of the marsh, whereas in many areas it dominates a distinct zone in the salt-marsh vegetation. Its limited rôle here may be due to the rapidity with which *Festucetum* develops, invading *Puccinellia maritima* directly and excluding intermediate stages.

However, comparison of the St. Cyrus marsh with other areas may be made, and in particular with Chapman's (1941) four groups. In a number of respects closer agreement is found with his "West Coast Marshes" than with the "East Coast Marshes". This is in accord with his observation that the marshes at Findhorn, in Nairnshire, fall into the west coast sere rather than that of the east coast, and the suggested reason is that they form on a very sandy soil. The typical east coast marshes, exemplified by those of East Anglia and the Wash, develop under the influence of extensive silting; while those of the west and apparently also the north-east coasts are characterised by a higher proportion of sand in the deposits. The particular features of the vegetation associated with these habitat conditions include the importance of *Puccinellia maritima* over extensive areas of the marsh and as the primary colonist, abundance of *Glaux maritima*, and the dominant rôle of *Festuca rubra*. It also appears from Chapman's diagrams that the development of a *Scirpetum maritimae* is more characteristic of the "west coast" seres than others.

A peculiar feature of the St. Cyrus salt-marsh is the importance of *Agrostis stolonifera*, which becomes dominant over considerable areas in the upper marsh. Chapman (1939) mentions this species only as an infrequent component of the East Anglian marshes, listing it in the *Juncetum maritimae* at Scolt Head. Yapp and Johns (1917), however, describe it as locally dominant in the *Festucetum* and abundant in the *Juncetum* in the Dovey estuary, but it does not figure in other accounts consulted. Its prominence at St. Cyrus may be accounted for by the widespread occurrence of very wet areas in the upper marsh, associated with rather low salinity.

Examination of the St. Cyrus marsh supports Chapman's general conclusion that the communities taking part in the sere are controlled to a considerable extent by the character of the soil. There is no doubt also that they are influenced by the relative frequency and duration of submergence in different parts of the marsh, as demonstrated by him (1934, 1938). These two factors together play a large part in determining both the moisture content of the substratum and its salinity. The present investigation emphasises the fact that all the species present on the marsh can withstand high salinities for short periods, but that relatively few can survive if such concentrations are maintained for any length of time. It does not seem that any of the species discussed here require high salt concentrations, since all are found in all parts of the marsh. Possibly it is only the pioneer colonist which has to withstand high salinities

for any length of time, since there is reason to believe that all the species encountered except *Puccinellia maritima* are adversely affected by continued exposure to salinities such as are frequently recorded at the lowest levels of the marsh (for *Armeria*, see Part I, vol. xxxv, p. 386). The effect of the pioneer colonist, however, is to raise the marsh level slightly, thus reducing submergence time, and to increase the silt proportion. Silt is more water-retentive than sand, and therefore concentration of the soil solution by evaporation from the surface is less evident. As the vegetation-cover becomes more complete, there is general reduction of surface evaporation. Although high salinities continue to be recorded at times under these conditions, they are much less likely to be prolonged and the typical salt-marsh communities are able to develop.

The species composing these communities are generally regarded as halophytes. If this term can properly be applied to them, it is evidently not because of any capability of flourishing in constantly high salinities. Nor can it be because they can withstand temporarily high salinities, since it is probable that many other species share this property, as indicated in connection with the rich cliff flora at St. Cyrus (Part I). Its justification must lie in their tolerance of widely fluctuating habitat conditions, including a general level of salinity somewhat higher than in other situations, and at least occasional rapid alternation between complete submergence and exposure to an atmosphere which at times may be strongly desiccating. The salt-marsh flora can compete in this habitat, which excludes other species, whereas their absence from other habitats is at least partly a result of failure in competition rather than inability to grow under any other conditions. The luxuriance with which many of these species grow in gardens adds strength to this view, while a few, such as *Plantago maritima* and *Armeria maritima*, have inland stations, as at high altitudes on mountain screes of basic material, where again competition from other species is reduced.

Reasons have been advanced for expecting lower values for the concentration of salt in the soil moisture at St. Cyrus than in many other salt-marshes, and confirmation is obtained by comparing the figures with Chapman's (1939) analyses of East Anglian marshes. Figures given by Morss (1927) for the Nith estuary (Solway Firth), however, are even lower than those for St. Cyrus, and these findings lend support to Yapp's (1917) statement that sandy salt-marsh soils are in general poorer in salt than those with high proportions of silt. This may be an added reason for the telescoped nature of the

sere, with communities belonging to the upper marsh invading the early stages.

Chapman (1941) stressed the need for autecological studies of salt-marsh species, as a key to the processes taking place. The present investigation has made a contribution in this direction, from which two general points arise. The first is that the distribution of several species within the marsh appears to be more directly related to the wetness of the substratum than to any other factors. This applies, for instance, to *Triglochin maritima*, *Aster tripolium* and *Atriplex babingtonii*, which are present in the frequently-submerged areas near the lower limits of the marsh, as well as the water-logged areas in the upper parts. Secondly, it is apparent that the species with the widest distribution over the marsh are those capable of much variation in growth-form. The difference in the growth-form of *Puccinellia maritima* when behaving as a colonist and as a dominant has been remarked, while the range of types to be found in *Glaux maritima*, *Plantago maritima* and *Cochlearia officinalis* is particularly noticeable. This range may be of considerable significance in enabling the species to play a part in several different types of community. The particular growth-form exhibited by *Triglochin maritima* plays a large part in determining the type of colony form and the associations with other species.

Further investigation of the autecology of salt-marsh species would be of great value in determining the conditions leading to the development of the different seres and controlling the balance between different dominants. In particular, there is need for re-investigation of salt tolerance, taking into account the response of each species to varying periods of time in contact with given salt concentrations.

SUMMARY.

An account is given of the salt-marsh at St. Cyrus, which is of relatively recent origin. The marsh connects with the present river channel of the North Esk, and as the tide fills it the flood water is somewhat diluted by river water. This fact, together with the sandy deposits and the presence of drainage water from land-ward, maintains salinities lower than in some other salt-marshes. Salinity may, however, remain fairly high for periods of some length at the lower end of the marsh, but decreases on passing upwards. Silt proportions are greatest in the centre and these help to retain water, while the sides are more sandy and freely drained.

Eighteen species belong to the flora of the marsh proper.

Puccinellia (Glyceria) maritima is the pioneer colonist, retaining an important position throughout the succession. Dominance, however, passes rapidly to *Festuca rubra* in drier parts, while *Agrostis stolonifera* occupies generally water-logged areas. Certain regions retain water for longer periods and are colonised by *Scirpus maritimus*. *Juncus gerardi* dominates a small area near the apex of the marsh. A zonation involving *Plantago maritima*, *Armeria maritima*, *Honkenya peploides* and other species is observed at the edges of the marsh.

Investigation of the rôles of the three grasses indicates that all occur together in some regions, but the balance between them is dynamic. *Festuca rubra* is a strong competitor in drier, sandy regions, and is actively invading the lower parts of the marsh. The autecology of *Aster tripolium*, *Cochlearia officinalis*, *Plantago maritima*, *Scirpus maritimus* and *Triglochin maritima* is discussed, with reference to the factors controlling their distribution. The significance of variability in growth-form in enabling some species to play a part in several community types is emphasised.

Like the marshes at Findhorn, in Nairnshire, the St. Cyrus marsh fits into Chapman's (1941) "West Coast Seres", owing to the sandy nature of its deposits. This, together with frequency and duration of submergence, determines the wetness and salinity of the substratum. It is suggested that, apart from the primary colonist *Puccinellia maritima*, the majority of the marsh species would be adversely affected by continued exposure to high salinities. Their presence as halophytes depends on ability to compete under conditions including salinity somewhat higher than in other habitats, and alternation between complete submergence and exposure to a drying atmosphere. Further investigation of salt tolerance should take into account the response of each species to varying periods of exposure to given salt concentrations.

APPENDIX.

FLORA OF THE MAIN AREA OF ST. CYRUS SALT-MARSH.

AGROPYRON PUNGENS (Pers.) Roem. &	JUNCUS GERARDI Lois.*
Schult.*	PLANTAGO CORONOPUS L.
AGROSTIS STOLONIFERA L.	P. MARITIMA L.
ARMERIA MARITIMA (Mill.) Willd.	PUCCINELLIA MARITIMA (Huds.) Parl.*
ASTER TRIPOLIUM L.*	SCIRpus MARITIMUS L.*
ATRIPLEX BABINGTONII Woods.	SPERGULARIA MARGINATA (DC.) Kittel.*
COCHLEARIA OFFICINALIS L.	S. SALINA J. & C. Presl.*
FESTUCA RUBRA L.	SUAEDA MARITIMA (L.) Dum.*
GLAUX MARITIMA L.*	TRIGLOCHIN MARITIMA L.*
HONKENYA PEPLOIDES (L.) Ehrh.*	

ADDITIONS TO ST. CYRUS FLORISTIC LIST (see vol. XXXV, p. 412).

Species marked with an asterisk (*) above.

CAREX OTRUBAE Podp.

PLANTAGO CORONOPUS L. f. PYGMAEA Lange. } Transitional region between salt-
SAGINA MARITIMA Sm. } marsh and fixed sand-dunes.

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OBSERVATIONS ON THE BRYOPHYTE FLORA OF THE
ISLE OF MAY.

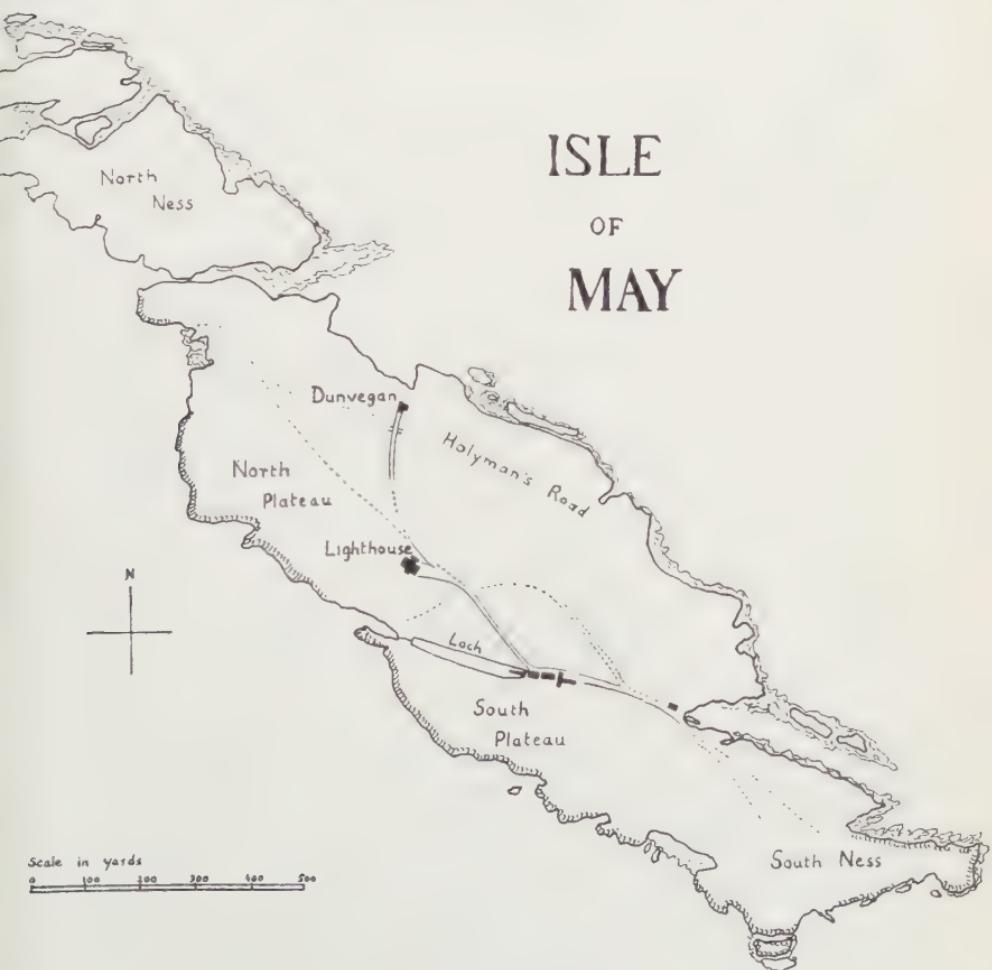
By E. V. WATSON.

(Department of Botany, University of Reading.)

(Read by title, 15th January 1953.)

INTRODUCTORY REMARKS.

The Isle of May (text-fig. 1) lies at the mouth of the Firth of Forth, about five miles distant from the coast of Fife and nine from the East Lothian coast at North Berwick. Rather over a mile in



TEXT-FIG. 1.

TRANS. BOT. SOC. EDIN., VOL. XXXVI, PT. II., 1953.

length, it is nowhere above one-third of a mile in breadth, and for the most part is considerably narrower. The total area, according to Rattray (1886), is 143 acres.

Geologically, the island consists of an intrusive sill of olivine-dolerite (Geikie, 1902). This rock outcrops in all parts of the island and produces formidable cliffs on the west coast. These cliffs reach 150 feet in height in places, the highest point on the Isle of May being 168 feet (site of the lighthouse). The North Ness is composed almost exclusively of rocky outcrops and at high water forms a series of separate islets. A deep gully farther south is the site of the freshwater loch. Some comparatively level land, where there are several fields at one time cultivated, represents a fragment of the 50-foot raised beach. There is a general west-east downward slope of the land as a whole; this is thought to conform with the dip of underlying sedimentary rocks, which are, however, nowhere exposed.

The climate is in many respects of the oceanic type, as is shown by the accompanying table of figures kindly supplied by the Scottish Meteorological Office of the Air Ministry. Thus there is a difference of only 17.7° F. between the January and July mean temperatures, there is no season of markedly reduced rainfall and the relative humidity is comparatively high at all times of the year, the highest mean figures over a twelve-year period being those for early morning (0700 hr.) in the later summer months. Whilst the mean annual rainfall (21.8 in.) is not high, the high relative humidity and the relatively low summer temperatures must do much to compensate for the effect of this from the standpoint of bryophyte vegetation.

The general vegetation of the Isle of May attracted the attention of numerous botanists during the nineteenth century, and papers were published by Sadler (1871) and Rattray (1886) dealing in some detail with the phanerogamic flora but paying no serious attention to the bryophytes. W. Evans (1908, 1910) was the first to give an account of the bryophytes of the island, and his work has furnished the foundation on which it has been possible to build the more comprehensive annotated list that forms the main substance of the present account. G. West (1910) made casual reference to certain mosses and hepaticas on the Isle of May, but he does not appear to have studied this element in the flora critically.

The principal purpose of the present paper is to bring the lists of Evans up to date, incorporating such additions to the bryophyte flora of the island as have resulted from small collections made by the present author in 1935, 1938, 1946 and 1949. Some study and

collecting of bryophytes has been carried out in each of the months April, May, June, August and September, but on no occasion was the island visited for more than a few days at a time and almost always the visits were undertaken primarily to carry out ornithological work at the well-known Isle of May Bird Observatory. Thus, in a sense, the account that follows rests on the results of a

TABLE I.

MEAN TEMPERATURE, PRESSURE, RAINFALL AND RELATIVE HUMIDITY RECORDS FROM THE FIRTH OF FORTH.

Months.	Isle of May.			Inchkeith.		
	Temp. (° F.).	Barometric Pressure (in.).	Rainfall (in.).	Relative Humidity (%)		
				1300 hr.	0700 hr.	1800 hr.
Jan.	39.0	29.808	1.6	83	88	86
Feb.	39.0	29.870	1.5	83	89	86
Mar.	39.9	29.826	1.7	78	89	81
Apr.	43.7	29.904	1.2	76	87	80
May	48.0	29.940	1.7	78	87	80
June	53.8	29.944	1.6	75	86	77
July	56.7	29.872	2.3	78	90	80
Aug.	56.7	29.855	2.7	76	90	80
Sept.	53.6	29.868	1.6	77	90	80
Oct.	48.0	29.813	2.2	78	87	83
Nov.	42.9	29.829	1.8	83	88	85
Dec.	40.0	29.800	1.9	85	89	87

Periods: Temperature, 1856-1895.

Barometric
Pressure, 1856-1895.

Rainfall,

Relative
Humidity,

1881-1915.

1923-1935.

series of casual collections, to which must be added a small collection kindly made by Dr. C. C. Balch in May 1951, and it would be rash to claim that the ground had as yet been exhaustively covered where organisms so easily overlooked as the smaller bryophytes are concerned. At the same time, in 1949, some attempt was made to formulate a picture of the available habitats for bryophytes on the island as a whole, and to piece together the groups of species, or communities if they merit the term, that had come into being there.

ECOLOGICAL CONSIDERATIONS.

As already indicated, the climatological data available suggest an environment suited, in general, to the development of bryophytes. Nevertheless, the range of habitats is restricted, and on an island as narrow as the May all sites must inevitably come under the influence of close proximity to the sea. Just how far this circumstance restricts the wealth of species in any given habitat it is difficult to say. Certain species, such as *Grimmia maritima*, *Tortella flavovirens* and *Ulota phyllantha* are well known to tolerate conditions existing within and just above the spray zone of maritime rocks, but with the wind strengths that prevail on the Isle of May one suspects that salinity of the atmospheric moisture must be an important factor influencing the vegetation even of the higher ground. Evans (1910) commented on the "numerous departures from the typical form" which he met with among the bryophytes on the island, and it may be that the maritime influence is felt more in this direction, *i.e.* in modifying the habit of existing species, than in restricting the number of species to be found.

A factor of considerable importance in shaping the character of the phanerogamic vegetation on the North Ness, and to some extent elsewhere, lies in the nitrogenous enrichment of the substratum that arises directly from the presence of very large and concentrated colonies of nesting sea-birds at these points. This interesting aspect, however, has not so far received attention bryologically; personal experience suggested that bryophytes were virtually absent over much of the North Ness where the great tern colony has fostered the development of a "nitrophile" element among flowering plants; but this point deserves study, as too does the influence, if any, of the cliff-nesting species (kittiwake, guillemot, etc.) on the bryophyte flora of the ledges where they breed.

Although Sadler (1871) referred to the rock composing the Isle of May as one "regarded by botanists as most productive", it hardly seems, at first inspection, to bear out this reputation in its bryophyte flora; for only some half-dozen species grow directly on these rocks, and even such widely distributed lithophilous species as *Grimmia pulvinata* and *G. apocarpa* have never been recorded from the island. Of the rock-dwelling species which occur, the most interesting are undoubtedly *Grimmia stirtoni* and *Frullania germana*. Both are plants that in Britain as a whole have a predominantly western distribution, and the interest of *F. germana* was remarked upon by Evans in his first paper, indicating as it did an oceanic element in

the bryophyte flora of the island. This species has not been found again, but *Frullania tamarisci* occurs in places on the rocks. Some difference of opinion appears to exist concerning the ecological status of this species. Doignon (1947) classes it as silicicole, but E. W. Jones (1952), commenting on the availability of suitable habitats for it in Berkshire and Oxfordshire, refers to it as a calcicole. On the Isle of May, in one station at least, it is associated with *Camptothecium sericeum*, a species which is often abundant on lime-rich rocks but is by no means confined to them. The small cave at the South Ness bears on its walls a rich growth of *Conocephalum conicum* (associated with the fern *Asplenium marinum*); the presence of the liverwort indicates reasonably base-rich conditions (Doignon, 1947; Hora, 1947; Jones, 1952). A consideration of the principal species occurring on the rocks has shown that whilst they are few in number they are nevertheless in keeping with the moderately base-rich substratum that one associates with a doleritic rock. It may be that proximity to the sea has itself exerted a restrictive influence on the wealth of lithophilous species to be found on the island.

The number of species growing on soil, including soil-capped rock ledges, is considerably greater. Several of these utilise small patches of bare soil, sheltered by tufts of grass or cushions of *Armeria* and other maritime plants. Sheltered niches of this kind occur on steep slopes in several parts of the island and form a fairly well-defined habitat where the following plants occur: *Barbula cylindrica*, *Eurhynchium praelongum*, *Dicranella heteromalla*, *Fissidens* spp. The steep, north-facing slope of the south bank of the loch and the irregular banks that rise above Holyman's Road in the east of the island provide two of the best examples of this habitat.

In several places locally impeded drainage has given rise to patches of marsh flora, whilst at some points more or less permanently moist conditions are maintained by means of small springs. Thus, *Acrocladium cuspidatum*, *Brachythecium rivulare* and paludal states of *B. rutabulum* occur in marshy ground near Dunvegan, on the east side of the island, and permanently moist sites at the cliff-top in the west are the habitat of *Bryum alpinum* and *Drepanocladus fluitans*. A single species of *Sphagnum* (*S. plumulosum*) was found at one point, on the South Ness, in September 1949. Small pools on the North and South plateaux, deprived of standing water but by no means desiccated in the dry summer of 1949, had a characteristic bryophyte flora. Often this consisted of a continuous, close carpet composed mainly of the liverworts *Nardia scalaris* and *Lophozia ventricosa*, with variable amounts of the moss *Dicranella*

heteromalla. One such site produced the only plants of *Anthoceros* (*A. laevis*) that I have found on the island. These subaquatic soil habitats would undoubtedly repay close study from anyone able to make frequent visits at all seasons of the year; the bryophyte carpets met with in September 1949 may well represent a transitory phase, in either an annual cycle of events or a more long-term succession.

Many soil bryophytes grow characteristically in the turf or on exposed soil laid bare by some local agent of erosion; that is, in either event, their abundance varies inversely with the general luxuriance of the vascular plant vegetation. Over-grazing, or any comparable agent of turf impoverishment, can exert an important influence on this element of the bryophyte flora and there seems little doubt that it has done so on the Isle of May. Eighty years ago Sadler referred to the great impoverishment that had taken place in the once fine turf of the island pasture as a result of the depredations of innumerable ants; and rabbits are known to have been abundant on the island at least as long ago as 1329 (Ritchie, 1920). Mr. J. H. B. Munro, to whom I am indebted for drawing my attention to this last reference, informs me that in his own long experience of ornithological work on the Isle of May he had at no time been struck by the abundance, or even the presence, of ants on the island until, in September 1949, migrant Northern Greater Spotted Woodpeckers were seen feeding on them. His view, which agrees with my own and that of other visiting observers, is that ants are indeed seldom noticeable on the May at the present time. Rabbits, on the other hand, continue to abound. Within recent years, too, the turf has unquestionably suffered from the increasing numbers of trippers and others visiting the island during the summer months. In some seasons (e.g. 1949) considerable areas have been fired and have continued to smoulder for weeks at a time. Thus, although ants would seem to have decreased and livestock (chiefly sheep) formerly pastured on the Isle of May are there no more, factors making for impoverishment of the turf and in places for erosion of the soil have continued in the ascendancy, in the shape of over-grazing by rabbits and firing of the turf by man. Table II illustrates changes in status of certain mosses which either grow in the turf or are associated with denuded soil surfaces. It will be noted that whilst two species show no known change in status and one has perhaps decreased, no less than five species show evidence of having increased since the period covered by Evans' observations. I have not been able to re-examine the areas of turf fired in 1949, but I

should be surprised if that event had not led to a further increase in several of these species.

TABLE II.

APPARENT CHANGES IN STATUS OF CERTAIN MOSES GROWING IN THE TURF, ISLE OF MAY.

Species.	Apparent Status, 1885-1910 (Evans, 1908, 1910).	Status, 1949.
<i>POLYTRICHUM JUNIPERINUM</i>	Very scarce	Locally plentiful
<i>P. PILIFERUM</i>	Not recorded	Locally plentiful
<i>CERATODON PURPUREUS</i>	Not recorded until 1910; then only on cinder heaps	On denuded sur- faces of plateau land
<i>DICRANUM SCOPARIUM</i>	Not recorded	Fairly widespread
<i>PSEUDOSCLEROPODIUM PURUM</i>	Not recorded	Present on banks
<i>RHYTIADIDELPHUS SQUARROSUS</i>	Very scarce	Not recorded
<i>POHLIA NUTANS</i>	No known change of status	
<i>MNITIUM HORNUM</i>		

Finally, reference may be made to one other group of habitats in which an increase of bryophyte flora might be expected to have taken place in recent years. This comprises the cinder paths and related man-made sites which have inevitably become more extensive on the Isle of May as the island has become increasingly populated and "developed". Even within the past fifteen years great changes have taken place in connection with the important part played by the island in World War II and the erection there of several new buildings. It is therefore of some interest to note the changes that have come about in the status of certain mosses of these habitats. In his first annotated list, based mainly on ten days' observations on the Isle of May in 1885, Evans (1908) recorded no *Tortula muralis*, *Bryum argenteum*, nor any species of *Barbula*. In his second paper (1910) he was able to report *T. muralis*, *B. argenteum* and *Barbula recurvirostris* (*B. rubella*) among other recent additions to the island flora, the first two only in small quantity but *Barbula recurvirostris* as "common on old track". In 1949 *Bryum argenteum* and *Tortula muralis* were widespread on these man-made habitats, and *Barbula recurvirostris* persisted on the path to Dunvegan, presumably the "old track" of Evans. In addition, *Barbula convoluta* was present at this latter station, where, as usually happens, its light green colour

made it conspicuous; *Barbula unguiculata* was recorded as a further addition to this "viatical" element in the flora, near the Naval Buildings which had been erected during the recent war.

ANNOTATED LIST.*

MOSSES.

†*SPHAGNUM PLUMULOSUM* Röll.

Taken in small quantity from a patch of moist ground among rocks, on the South Ness.

POLYTRICHUM PILIFERUM Hedw.

Collected in 1946 and again in 1949, in the latter case from fairly high ground near the old observatory.

P. JUNIPERINUM Hedw.

Collected with capsules nearly ripe, April 1935; taken again in 1946. In 1949 it was noted with *Dicranum scoparium* and *Ceratodon purpureus* on eroded surfaces, North Plateau; also on the slope above Holyman's Road.

FISSIDENS VIRIDULUS (Web. & Mohr.) Wahl.

Recorded by Evans.

†*F. BRYOIDES* Hedw.

Taken in small amounts, with *Mnium hornum* and *Eurhynchium praelongum*, on the steep north-facing slopes above the loch (1949).

†*ARCHIDIUM ALTERNIFOLIUM* (Hedw.) Schp.

On a patch of wet ground in the hollow of rocks, on the South Ness, 31st August 1949. Antheridia and archegonia were found in the young "inflorescences".

CERATODON PURPUREUS (Hedw.) Brid.

Comparatively ill-developed plants were taken from eroded surfaces, on the North Plateau, in August 1949.

DICRANELLA HETEROMALLA (Hedw.) Schp.

Taken, with mature capsules, from a shaded hollow in the grass-land of the North Plateau, March 1938. It also grows elsewhere

* The nomenclature and arrangement of mosses follows the check-list of Richards & Wallace (1950); the liverworts conform with the check-list of Buch, Evans and Verdoorn (1937).

† Species not hitherto recorded from the Isle of May.

on the island, on soil in the shade of grass tussocks, notably in Holymans Road, where luxuriant plants with young capsules were collected on 1st September 1949.

†**DICRANUM SCOPARIUM** Hedw.

Not abundant, but occurred (1949) on the rocky hillside west of Holymans Road, near the old observatory, and on parts of the North Plateau.

TORTULA MURALIS Hedw.

Along cinder paths and similar places.

POTTIA HEIMII (Hedw.) Furnr.

Taken on 30th June 1946 from steep banks by the loch. Capsules were present in various stages of ripeness.

P. ASPERULA Mitt.

Recorded by Evans.

†**BARBULA CONVOLUTA** Hedw.

Plentiful along the path to Dunvegan, where its bright yellowish-green colour makes it stand out among the tufts of the associated *B. recurvirostris*. First Record, June 1946.

†**B. UNGUICULATA** Hedw.

One large tuft taken from waste ground by the Naval Buildings, September 1949.

†**B. TOPHACEA** (Brid.) Mitt.

Collected on the banks of the loch, June 1946.

†**B. CYLINDRICA** (Tayl.) Schp.

Found in small amounts on soil, on shaded ledges of the steep north-facing bank of the loch, associated species being *Eurhynchium praelongum* and *Mnium hornum*. The dominant flowering plant on much of this embankment is *Ligusticum scoticum*.

B. RECURVIROSTRIS (Hedw.) Dix.

In some quantity along the cinder path to Dunvegan.

TORTELLA FLAVOVIRENS (Bruch) Broth.

On rock ledges, notably by the loch.

GRIMMIA MARITIMA Turn.

Locally plentiful round the rocky coast of the island, this species occurs in notably large amounts on the rocks near the East Landing.

G. STIRTONI Schp.

This species has been found only on rocky outcrops on fairly high ground between Dunvegan and the old observatory. It is quite plentiful there.

FUNARIA HYGROMETRICA Hedw.

Fertile plants were found on the path by the loch in May 1946.

PHYSCOMITRIUM PYRIFORME (Hedw.) Brid.

Recorded by Evans.

POHLIA NUTANS (Hedw.) Lindb.

Plants without capsules, but showing the paroecious inflorescence, were collected on the South Plateau, August 1949.

[BRYUM INCLINATUM (Brid.) Bland.

Of a specimen submitted by Evans in 1904 the late H. N. Dixon wrote "probably *inclinatum*, but impossible to say certainly in absence of fruit". I have collected barren material which seems best referred to this species. It was taken on rocks by the East Landing.]

†[B. INTERMEDIUM (Ludw.) Brid.

Some plants collected by the author in June 1946 were considered by Mr. J. B. Duncan to be probably this species. Although the plants were fruiting, all the capsules were either too young or too old for the peristome to be satisfactorily studied.]

B. ARGENTEUM Hedw.

In his second paper Evans records finding this species in June 1909 on "the track near the harbour", and the fact that it was not mentioned at all in his first list indicates that it must have been a scarce plant on the island forty years ago. In 1946 I found it plentiful, ample barren material occurring on the path by the loch and good fruiting specimens along the cinder path to Dunvegan.

B. BICOLOR Dicks.

On paths and on the dried-out beds of pools on the high ground. One form from this latter habitat was considered by Mr. J. B. Duncan to be very close to var. *gracilentum* Tayl. ex. Braithw.

B. ALPINUM With.

Evans noted the presence of this interesting species on the island as long ago as 1885, and collected it again in 1899. It may still be

found, forming luxuriant patches on marshy ground at the western edge of the North Plateau and in a similar situation on the South Plateau. Evans commented on the occurrence of a form "approaching var. *viride*", and I have myself obtained what is probably the same plant. It is a pure bright glossy green in colour and has leaves nearly twice as wide as those of the typical form. The cells, moreover, are both wider and on the average longer than in typical *B. alpinum*.

B. CAPILLARE Hedw.

Recorded by Evans.

MNIUM HORNUM Hedw.

This species is fairly plentiful, not only on steep, sheltered banks, but also among rocks in more exposed places in some parts of the island. As early as 1885 it was found by Evans, who commented on the small size of the plants, which were invariably barren. On comparing the leaf-cell structure of plants from the Isle of May with that of *M. hornum* from ordinary woodland habitats, I have found that the former differed in their smaller cells, with thicker walls. The thickenings at the corners of the cells are in some instances very marked, whereas absence of such thickening is usually regarded as a character of typical *M. hornum*. It should be stressed that *M. hornum* is growing on the Isle of May in some habitats which must be considered somewhat abnormal for the species, e.g. among rocks quite close to the sea in the south-east of the island, and whilst soil moisture and atmospheric humidity must be adequate in such a situation, it would tend to be a rigorous habitat in other respects, such as exposure to full sunlight and to winds frequently laden with salt spray. It would be interesting to see what became of these plants in cultivation.

ULOTA PHYLLANTHA Brid.

It is widely distributed on rocky outcrops, and has been collected by the loch, on the North Plateau and on the North Ness. In this last locality I collected it on 1st September 1949, together with *Grimmia maritima*, on rocks in the *Xanthoria* zone, only a few feet above high-tide level. The only Angiosperms nearby were a few scattered cushions of *Armeria maritima*.

[**CAMPYLIUM CHRYSOPHYLLUM** (Brid.) Bryhn.

Reported by Rattray, but the record has never been confirmed subsequently.]

[C. POLYGAMUM (B. & S.) Lange & C. Jens.

In 1910 Evans reported finding a plant which Dixon considered to be "probably *Hypnum polygamum*, though somewhat abnormal". I have been unable to trace this specimen in the Herbarium of the Royal Botanic Garden, Edinburgh, and the record may perhaps be felt to be in need of confirmation.]

DREPANOCLADUS FLUITANS (Hedw.) Warnst.

First recorded by Evans in 1909, when he found it to be abundant in pools on the South Plateau. I have found forms of this variable species to be widely distributed in suitable habitats.

ACROCLADIUM CUSPIDATUM (Hedw.) Lindb.

Recorded by Evans in 1910, it may still be found in the marshy ground near Dunvegan.

ISOTHECIUM MYOSUROIDES Brid.

In 1885 and again in 1908 Evans collected a large form, said by Dixon (*in lit.*) to approach the var. *brachythecioides*. I have been unable to confirm the presence of either the typical form or the variety.

CAMPTOTHECIUM SERICEUM Kindb.

First recorded by Evans in 1910. I have taken it from what appears to be the identical station—rocks flanking the path to Dunvegan, in August 1949. So far it has not been found elsewhere on the island.

†BRACHYTHECIUM ALBICANS (Hedw.) B. & S.

The only record appears to be one small gathering, made by myself in April 1935.

B. RUTABULUM (Hedw.) B. & S.

Evans, recording it in 1885, remarked that it was "scarce and barren". I have found it in small quantity by the loch. I have found in addition what appears to be a paludal state of this species, also without capsules, in some abundance on wet ground in a depression just south of Dunvegan.

†B. RIVULARE (Bruch) B. & S.

Collected in 1949 by myself, and again in 1951 by Dr. C. C. Balch, on marshy ground just south of Dunvegan.

B. VELUTINUM (Hedw.) B. & S.

Recorded by Evans in small quantity, but not found subsequently.

B. PLUMOSUM (Hedw.) B. & S.

In his second paper Evans recorded finding a little among *Grimmia maritima*. I have not seen it on the island.

EURHYNCHIUM PRAELONGUM (Hedw.) Hobk.

Recorded by Evans in 1885 and mentioned by Rattray in 1886. This is one of the commonest mosses on the island in shady situations. Thus it occurs, with *Mnium hornum*, *Fissidens bryoides* and *Barbula cylindrica*, on the steep, north-facing bank of the loch. It is widely distributed on earth surfaces that are shaded by rock or grass, and is associated with *Conocephalum conicum* on the sides of the small cave on the South Ness. It also grows with *Acrocladium cuspidatum* on the marshy ground below Dunvegan, where it was found with capsules in 1946.

[E. CONFERTUM (Dicks.) Milde.

Reported by Rattray, but the record has never been subsequently confirmed.]

PSEUDOSCLEROPODIUM PURUM (Hedw.) Fleisch.

Found, among grass, on steep banks on the west side of Holyman's Road, near the bridge to Dunvegan, September 1949.

PLAGIOTHECIUM UNDULATUM (Hedw.) B. & S.

Evans found it in 1910 in the moist hollow by Dunvegan. I have not met with it.

HYPNUM CUPRESSIFORME Hedw.

Plants approaching typical *H. cypresiforme* were collected by the path to Dunvegan in August 1949.

var. RESUPINATUM (Wils.) Schp.

Evans recorded this variety (as *Hypnum resupinatum*) in 1910, stating that it occurred sparingly on rocks near the south end of the island. It was collected by me on the North Ness in 1949, growing a few feet above high-water mark with *Grimmia maritima* and *Ulota phyllantha*, in the *Xanthoria* zone of the maritime rock vegetation.

var. ERICETORUM B. & S.

Evans in his earlier paper (1908) remarked that all the material of *H. cypresiforme* found by him was "either var. *ericetorum* or near

it". In 1935 I collected plants which Mr. J. B. Duncan agreed were referable to this variety.

RHYTIDIadelphus squarrosus (Hedw.) Warnst.

Evans reported finding "a very little" in September 1885. One would expect it to occur, but it has not appeared in my own collections so far.

LIVERWORTS.

LEPIDOZIA REPTANS (L.) Dum.

Recorded by Evans. I have no material of it.

CALYPOGEIA TRICHOMANIS (L.) Corda.

Recorded by Evans. I have come across fragments among other liverworts on damp soil on parts of the South Plateau.

CEPHALOZIELLA sp.

A record by West (1910) of *C. Starkii* (Funck.) Schiffn. must be accepted with caution. Barren stems of *Cephalozziella* sp. have appeared in my own collections of other liverworts from damp ground.

LOPHOZIA VENTRICOSA (Dicks.) Dum.

Probably the most generally abundant liverwort on the island. It was recorded by Evans as early as 1885. In 1949 I found it to be the chief species in a liverwort associes that carpeted the vertical banks of dried-out shallow pools on the North Plateau. It was also abundant and luxuriant on the grassy ledges flanking the northern extremity of Holyman's Road. Whether or not any of the plants are referable to the very closely allied *L. silvicola* Buch. it is not at present possible to say.

NARDIA SCALARIS (Schrad.) Gray.

Reported by West in 1910, and taken in 1949 from moist ground in a shallow gully on the South Plateau.

[LOPHOCOLEA BIDENTATA (L.) Dum.

This species was reported by West in 1910. Evans remarks that Macvicar, examining his collections of *Lophocolea* sp. from the island, pronounced that some *may* have been *L. bidentata*, but conclusive evidence in the shape of the inflorescence was lacking. It is still not possible to confirm the presence of this species.]

L. CUSPIDATA (Nees) Limpr.

Recorded by Evans and found by myself in several places.

PLAGIOCHILA ASPLENIOIDES (L.) Dum. var. *humilis* Lindenb.

Recorded by Evans, but not found subsequently.

CEPHALOZIA BICUSPIDATA (L.) Dum.

Recorded by Evans. I have met with fragmentary material of it among other liverworts on moist soil.

FRULLANIA GERMANA Tayl.

Evans commented on the special interest attaching to the occurrence of this oceanic species on the Isle of May. It has not been found by me.

F. TAMARISCI (L.) Dum.

Locally plentiful on rocks.

CONOCEPHALUM CONICUM (L.) Dum.

This conspicuous liverwort was noted by Rattray (1886) and has been observed by all subsequent bryologists who have visited the small cave where it still grows, under the cliff-top at the South Ness.

[LUNULARIA CRUCIATA (L.) Dum.

Evans, in his second paper, remarked that he looked in vain for this species in the cave at the South Ness where West reported it as growing. I, too, have failed to find it, and it seems possible that West may have been misled by smaller, paler states of the last species, which assumes both large and small forms in that cave.]

†ANTHOCEROS LAEVIS L.

Found in September 1949 in small quantity on the mud of partially dried-out pools on the North Plateau.

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